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THE TERTIARY CHARACTER OF THE COVE HARDWOOD FORESTS OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK[1]

STANLEY A. CAIN

It is the purpose of this paper to show by indirect means that large numbers of the genera of the cove hardwood forests are ancient genera whose species have long lived in the southern Appalachian region. In order to develop the probability of this thesis, it is necessary to make certain assumptions. Direct evidence is lacking.

Abundant fossils of angiospermous forms appear in the Cretaceous, and in the later Cretaceous the flora had become pretty thoroughly modernized with respect to families and genera of flowering plants. Throughout the long history of angiospermous evolution, the southeastern highlands of the United States have been continuously available for occupancy by plants. At longer or shorter intervals of time during this period overland highways have been available for plant migration. The modern flora shows relationships with the south—the Caribbean, Mexico, and Central and South America—, with the north, and, by means of northern routes, with western American, eastern Asia, and Europe. Plant genera which undoubtedly originated elsewhere have found their way into the southern states; and from this area migrations have carried some stocks to remote regions. At other times connections have been broken by encroachment of seas upon the land—as by the Mississippi Embayment—or by ice from the north. Continental shelves have been submerged and coastal plains built up.

Unfortunately, however, the fossil record during this time is absent for the southern highlands themselves. It is only by indirection that we can know the nature of the flora of this region. Rather abundant Cretaceous and early and middle Tertiary fossils are available in the southeastern states, but only for lowland floras where land and sea have met and suitable sedimentary basins have been available.

Of the 81 genera that made their appearance in the Eocene Wilcox flora, 60 per cent are tropical in their modern affinities, and probably also in their ancestry, according to Berry (1930). The Oligocene, he said (Berry 1923), was "a time of tropical marine deposits along the southern coast." And although the "Miocene was pre-eminently the period of hardwood forests," the upland flora was undoubtedly scantily represented in the coastal deposits.

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In the following tables and calculations of percentages only fossil records from the southeastern states have been considered. Had records from western North America, Greenland, Europe, and Asia been employed, many additional genera could be added to those known from the Cretaceous and Tertiary of the southeastern states. It seems reasonable to assume, however, that several genera of more northern areas, characteristic of temperate and cool temperate climates, must have found their way southward in the uplands even while the shores of the Gulf were clothed by species of *Ficus*, *Cinnamomum*, *Laurus*, and other genera of warm temperate and subtropical nature. This assumption is warranted by the observation of modern distributions. For example, red spruce that reaches sea level in Maine does not go lower than 4–5,000 feet in the Great Smoky Mountains. At lower latitudes the same species or ecologically equivalent plants must live at higher altitudes in order to find environmental conditions to which they are adapted.

It is assumed, then, that the incomplete record of modern southern Appalachian genera in the Cretaceous and Tertiary deposits of the southeastern states is not necessarily due to their absence from the southeastern states (or from their chance absence from such floras as the Wilcox, or their lack of discovery as fossils), but is due to their remoteness in the southern uplands from suitable sedimentary basins. It seems to be more surprising that as many temperate genera occur as do, rather than that certain ones are absent from the fossil records. What chance, for example, would *Picea rubens* and *Abies Fraseri* of the present boreal forest of the Smokies have to enter a modern sedimentary basin at low elevation?

The use of the latitude-altitude relation is based on the assumption that the species of the past had approximately the same climatic requirements as do species of the same genera today. Generally this assumption is valid although it is well known that tropical genera and families may have occasional truly temperate forms, or the reverse, that temperate genera and families may have some tropical representatives. This assumption is at the heart of the principle of synchronization in the dating of geological floras as discussed by Chaney (1936). For example, when the Eocene redwood forest was in Alaska, a subtropical flora occupied Washington and Oregon. By Miocene time the redwood forest had migrated down the coast to replace the subtropical, but undoubtedly many of the temperate forms of the Miocene redwood forest of the John Day basin came not only down from the north but also down from higher elevations of approximately the same latitude. This ecological interpretation is valid, but the assumption that all deposits with the same flora are synchronous is not valid.

The second major assumption involved in the present thesis is that the ancient nature of certain genera can be deduced from modern areas. It is

not the size of a generic area that is important, but whether the total area is interrupted by major disjunctions wider than the dispersal capacities of the forms concerned. For example, on the American and Eurasian continents the Pleistocene ice sheets produced disjunctions of once transcontinental ranges. Western and eastern American species of several genera are no longer in contact, and many genera once in western as well as eastern North America are no longer represented west of the Great Plains (Fernald 1925). Similarly, many species were forced to withdraw from great portions of their Eurasian ranges with the continental ice advances and, especially in Europe, there was considerable extinction (Lippmaa 1938).

Long before the Pleistocene, however, the break-up of once circumboreal ranges had commenced in certain regions. From the London Clay flora, for example, it is seen that the subtropical elements were withdrawing from western Europe and being replaced by temperate forms; and in the later Tertiary many of the temperate ranges were disrupted. In America the disruption of transcontinental ranges had been going on steadily with the progressive desiccation of the continental interior by the barrier to the moisture-laden winds from the west formed by the Cordilleras.

Whatever the time of the transoceanic connections (whether by land bridges, as was undoubtedly the case in more recent times, or by continental displacement), two points are clear. In the first place, such connections across the north Pacific and the north Atlantic undoubtedly once existed; and second, climatic conditions were more favorable than now, because temperate plants can only migrate through regions of temperate climate. Demonstration of a land bridge does not prove a migratory tract—conditions must be suitable for the plants under consideration.

It is thus reasonable to assume that certain types of modern areas could only have been attained in Cretaceous and early Tertiary times. This applies with conspicuous reasonableness to those genera which today have species only in eastern North America and in eastern Asia; and applies with only slightly less certainty to those genera that have species of circumboreal area. As a matter of fact, in the absence of fossil records, it is only of those genera that are strictly American endemics, and especially when confined to the Atlantic half of the continent, that one cannot certainly say that they are as old as the Tertiary.

The assumption has been made that many temperate genera not known from the early Tertiary deposits of the southeastern states existed in that region at higher elevations than the floras represented by the Wilcox. It is necessary, then, to consider whether such uplands probably existed, for if there is evidence of their presence the assumption that they were covered by a temperate flora has a high degree of probability. It is true that when subtropical and warm temperate floras were in the lowlands of the south-

eastern states warm types also penetrated low-lying areas much farther northward, as at Brandon, Vermont. Synchronous with these invasions was a northward extension of temperate types to relatively high latitudes. At the same time there must have been an upward migration in mountainous regions of all vegetational belts. The problem, then, is whether there were in the southern states any land masses of sufficient elevation to have supported temperate floras during the early Tertiary and permitted an interdigitation of climatically different floras.

This seems to be a difficult question to answer, but some indication of the situation is obtainable from Wright (1932). The oldest erosion surface that is well preserved in this region is the Schooley peneplain. This erosion level stands today at about 3,100 feet at Pisgah and 4,000 feet near Grandfather Mountain, North Carolina. Certain mountain groups, supposedly as monadnocks, rise above the well developed Schooley level in nearby areas. For example, Grandfather Mountain now rises about 2,000 feet above the Schooley level, and Blue Ridge and Great Smoky Mountain peaks rise from 1,000 to more than 3,000 feet above the Schooley level at Pisgah. In addition to this differential in altitude, which may be conservatively placed at 2,000 feet, it is certain that the monadnocks were even higher above sea level. In places the slope of the Schooley peneplain appears to have been as much as 70 feet in a mile. Although its average slope was probably much less, it seems probable that the upper edge of the plain must have stood at somewhat more than 1,000 feet above sea level. There may have been some differential uplift which has made the Blue Ridge and other monadnocks higher now than they were in Schooley time. It does not seem unreasonable, however, to conclude that various monadnocks such as the Cumberland Mountains, the Great Smoky Mountains, and the Blue Ridge must have stood from 1,000 to 3,000, or even 4,000 feet above sea level. Two further questions need to be considered. Are these probable elevations sufficient to have permitted a temperate montane flora when the lowlands were occupied by warm temperate and subtropical floras? Were these elevations in existence during early Tertiary time?

Wright (1932) suggests that the Schooley is possibly Cretaceous. Cole (1941), who has studied the various erosion surfaces and made correlations of them, accepts the conclusion of Stose (1940) that the development of the Schooley surface can probably be assigned to the Jurassic, although the maximum dissection of this surface may not have occurred until mid-Tertiary. It is possible to conclude, then, that the Schooley was undergoing elevation during the Cretaceous and early Tertiary, and that the conclusion with respect to the presence of uplands in the southeastern states is fairly sound.

As to the other question, and judging from the altitudinal relations of

modern vegetational belts, it seems likely that the maximum elevations of 3,000 to 4,000 feet above sea level which the more important monadnocks probably had were sufficient to permit the existence of temperate vegetation in a latitude where subtropical floras occurred at sea level. This, as has already been admitted, does not constitute more than circumstantial evidence for the existence of a typical temperate flora in the uplands at Wilcox latitudes, but in view of the fact that the Wilcox does contain some temperate genera, it seems reasonable that the uplands must have contained many of them.

The method of obtaining the data presented below will be described briefly. A list of the arborescent species of the Great Smoky Mountains National Park was obtained from the Park catalogue (Jennison 1938). All other records of the flora are incomplete, because they represent only those plants encountered on sample plots from the cove hardwood forest complex. The list of trees and tabular data were obtained from plots that averaged about 4,000 sq. m. in area from each of 31 stations in the virgin forest of the Greenbrier region. Data concerning shrubs, woody vines, and herbs were obtained from 19 stations. During the spring-flowering season, 10 stations were studied by a series of 10 quadrats of 1 sq. m. each at each station. During the summer season, 9 stations were studied by a series of 10 quadrats of 6 sq. m. each at each station. Although these data do not include all the species of the cove hardwood forest complex, they do represent its characteristic composition in primeval condition.

Fossil records of the genera of the plants that compose the present forest were obtained from various publications concerning the southeastern states. This area is interpreted as extending from the deposits of the eastern shore of the Mississippi Embayment to Florida and northward to Kentucky, New Jersey, and Maryland. The formations consulted are shown in table 1. Only those records which seem certainly to represent modern genera are included. For example, *Gleditsiophyllum* is not accepted as indicating the presence of *Gleditsia*.[2] The publications used were principally those of Berry and Knowlton, and are cited at the bottom of table 7. In the study of modern generic areas Dalla Torre and Harms (1900–1907) provided the standard source of information. This was supplemented by reference to Bailey (1933), Small (1933), and other more recent sources.

If a genus is listed as being present in Asia and America, and absent from Europe, it frequently is confined to eastern Asia and eastern North America. Some species may occur also in the Himalayas or western North America, or in the south temperate zone. These additional areas do not affect the point made, that the genus has major disjunctions that are substantial

[2] Berry (1930) transferred *Cassia mississippiensis* to *Gleditsia ? mississippiensis* as a tentative disposal of certain Wilcox fossils.

proof of the ancient origin of the generic stock. *Hystrix*, for example, consists of four species in North America, Siberia, and New Zealand. *Vagnera* is in Asia and both western and eastern North America. *Arisaema* is in Asia, Abyssinia, and North America. *Podophyllum* is in America and the Himalayas. *Meibomia* is in America, Asia, and Australia. Sometimes the present disjunctions are partially bridged by fossil records. Section *Saccharina*, of *Acer*, according to Pax (1926), was represented in Europe and Pacific North America during the Tertiary. Today the section (or the genus *Saccharodendron*) consists of *A. saccharum*, *A. floridanum*, *A. nigrum*, and *A. leucoderme* in eastern North America, *A. grandidentata* in the Rocky Mountains, and *A. diabolicum* in Japan. A considerable number of the genera not only had an extensive range in the Cretaceous or early Tertiary, but probably also consisted of many more species than today. Not only are several genera represented today by a small number of closely related species in eastern America and eastern Asia, but these relic genera are frequently quite without close relatives. *Caulophyllum* has one species in each region. This is likewise true of *Tovara*, *Diphylleia*, *Sassafras*, and *Liriodendron*. When certain other genera are listed as being circumboreal, in Europe, Asia, and North America, it does not necessarily mean that the genus lacks tropical or south temperate species. *Carpinus*, for example, is also in the temperate of Mexico. *Wallia* (*Juglans*) is also in the West Indies and the Andes of South America. *Alnus* is also in the Andes; and *Morus* and *Ulmus* extend into tropical mountains. *Aster* is in South Africa, as is *Oxalis*. Many genera are practically all over the world, as well as being circumboreal. Here may be mentioned such genera as *Ranunculus*, *Poa*, *Carex*, *Senecio*, *Alsine* (*Stellaria*), *Galium*, *Allium*, *Cuscuta*, *Geum*, *Peramium* (*Epipactis*), etc.

TABLE 1. *Formations of the southeastern states checked for fossil representatives of the modern genera of the cove hardwood forests of the Great Smoky Mountains National Park. From Knowlton (1919).*

Age	Middle Atlantic	South Atlantic	Gulf
Pleistocene	Talbot Sunderland	Chowan Sunderland	
Pliocene			Citronelle
Miocene	Calvert		
Eocene		Barnwell	Claiborne Wilcox-Lagrange Midway
Cretaceous, Upper	Monmouth Matawan Magothy Raritan	Black Creek Middendorf	Ripley Eutaw Tuscaloosa Woodbine
Cretaceous, Lower	Patapsco Arundel Patuxent	Patuxent	Trinity

SOME CHARACTERISTICS OF THE COVE HARDWOOD FORESTS

The author has been studying the composition and structure of the virgin cove hardwood forests for the past several years and considerable unpublished data have accumulated. Quantitative studies have been made at over 50 stations, but the data employed in the present connection represent the summary of only 31 stations from the Greenbrier region. Single plots, averaging about 4,000 sq. m. in area, have been used for the arborescent layer. Occasionally the plots have been as small as 3,000 sq. m., or as large as 5,400 sq. m. The size of the plot at any station has been regulated by several factors: the size and density of the dominant species; the number of species in the community; and the homogeneity of the stand, with respect to frequency of the species and their basal area. It is thought that the data obtained from the various plots are more directly comparable, because of the adjustment of plot size to stand character, than if a constant-size plot had been used. Each plot was approximately of minimal area size.

The various subtypes of the cove hardwoods have been arranged in two alliances, the Aesculion and the Tsugion. The following tabulation shows the subtypes in each alliance:

Cove hardwood forest complex (Greenbrier region, Great Smoky Mountains)
- Aesculion
  - Aesculo-Tilietum (buckeye-basswood segregate)
  - Saccharodendro-Halesietum (sugar maple-silverbell segregate)
  - Betuletum (yellow birch segregate)
  - Fagetum (beech segregate, mostly a high altitude gap type)
- Tsugion
  - Tsugo-Fagetum (hemlock-beech segregate)
  - Tsugo-Liriodendretum (hemlock tulip tree segregate)
  - Tsugetum (hemlock segregate)

These forest types can be considered association segregates, in the sense of Braun (1935), or lociations, in the sense of Clements (1936) and Cain (1939). Collectively, the cove hardwood forests represent a southern Appalachian faciation of the maple-beech-hemlock-birch association of the eastern deciduous forest formation. The southern faciation is distinguished from the northern forest by the presence of such trees as *Aesculus octandra*, *Halesia monticola*, and *Magnolia Fraseri*, and the abundance of *Liriodendron tulipifera*. Most of the stations studied by quantitative means were selected because of their representation of the subtypes. A larger total acreage is covered by mixed, mesophytic forests that cannot be easily assigned to a subtype. This is the undifferentiated deciduous forest climax of Braun (1935), and others.

The concept is widely prevalent that the so-called Arctotertiary forest was essentially an undifferentiated mixture of a large number of temperate forest species. With relative homogeneity, it presumably occupied an ex-

tensive circumboreal territory, and, during the Tertiary, with climatic deterioration in many places, specific and generic ranges were contracted and disjoined. This process was brought virtually to a modern condition by the Pleistocene ice sheets. It is certainly true, as shown by fossil records as well as modern areas, that many species and genera once occupied more extensive areas; and many regions once had a richer temperate forest flora. For example, many eastern forest genera were once a part of the western American forests, and are now completely unrepresented there. It does not seem correct, however, to emphasize too strongly the undifferentiated character of the Tertiary forests. Inasmuch as there were oceanic and continental areas, low and high elevations, and strong topographic contrasts during the Tertiary, there must also have been local or microclimates. The Tertiary forest must also have had faciations and lociations, as well as larger associations. It is not intended to deny that the undifferentiated forest probably occupied a larger area during the Tertiary than it does today, but to emphasize that association segregates were undoubtedly a feature of the Arctotertiary forest then, even as now. To reason otherwise would be to assume that many species have changed their ecological tolerances, with the passage of time, always in the direction of narrower amplitude.

In table 2 are presented the statistical data concerning the arborescent layer. Density and coverage data are not shown for the purposes of this paper. By present (columns 1 and 3) is meant that the species was found growing within the number of plots indicated. A species was not considered to be dominant unless it composed about 50 per cent or more of the total basal area of the trees on the plot. Codominants are those species of more than about 15 per cent basal area. In most of the stations there were only about from two to four dominants and codominants making up 80 per cent or more of the stand. Constancy per cent is an indication of the occurrence of the species at the stations on a basis of the minimal area plots. From the table it is seen that 12 species are dominant or codominant at various stations in the cove hardwood forest. The two alliances are not distinguished by the presence or absence, but by relative importance of species. The most frequent dominants of the Aesculion are *Aesculus octandra* dominant at 10 stations, *Tilia neglecta* at 9 stations, and *Saccharodendron barbatum* at 8 stations. The most frequent dominants of the Tsugion are *Tsuga canadensis* at 12 stations and *Liriodendron tulipifera* at 9 stations. Twenty additional species are associates of the dominants, and do not attain sufficient coverage at any station to be classified as even a codominant. *Tsuga canadensis, Betula alleghaniensis, Aesculus octandra, Halesia monticola, Tilia neglecta, Saccharodendron barbatum,* and *Fagus grandifolia* have a constancy of class V, being present in the sample plots of more than 80 per cent of all the stands.

Shrubs and woody vines were sampled in the same plots employed for

TABLE 2. *Trees of the cove hardwood forests of the Great Smoky Mountains found on sample plot studies of the Aesculion and Tsugion.*

All genera were in the Southeastern States in Pre-Pleistocene except those marked by an asterisk:

	Aesculion (18)		Tsugion (13)		Cove Hardwoods
	Stations Present	Stations dominant or co-dominant	Stations Present	Stations dominant or co-dominant	Constancy %
Tsuga canadensis	16	4	13	12	93.5
Betula allegheniensis	16	3	10	0	87.1
Aesculus octandra	16	10	11	0	87.1
Halesia monticola	14	3	13	3	87.1
Tilia neglecta	16	9	10	1	83.9
Saccharodendron barbatum	15	8	10	0	80.6
Fagus grandifolia	14	2	11	4	80.6
Fraximus americana	10	1	9	0	61.3
Liriodendron tulipifera	5	1	9	9	45.2
Padus virginiana	7	1	2	0	29.0
Castanea dentata	3	1	3	1	19.3
Picea rubens	1	0	1	1	6.4
Magnolia Fraseri	3		12		48.4
Rufacer rubrum	3		10		41.9
Acer pennsylvanicum	6		6		38.7
*Tulipastrum acuminatum	6		4		32.2
Hicoria cordiformis	6		2		25.8
Amelanchier laevis	3		5		25.8
Acer spicatum	6		2		25.8
Ilex opaca	0		6		19.3
Quercus maxima	4		1		16.1
Svida alternifolia	3		2		16.1
Betula lenta	0		5		16.1
Hamamelis virginiana	1		2		9.7
Wallia cinerea	2		0		6.4
Ilex monticola	0		2		6.4
Aralia spinosa	0		2		6.4
Cynoxylon floridum	1		0		3.2
Cladrastis lutea	0		1		3.2
*Oxydendrum arboreum	0		1		3.2
Quercus montana	0		1		3.2
*Robinia pseudoacacia	0		1		3.2
Total number of species sampled	24		30		32
Total number of genera sampled	21		26		28
Total Tertiary genera sampled	19		22		24
Per cent genera sampled that are as old as the Tertiary	90.5		84.6		85.7

the herbaceous layer. Ten stations were studied during the spring flowering season, and nine additional stations were examined during the summer. These stations were taken mostly from the Aesculion. Table 3 shows that

TABLE 3. *Shrubs and woody vines of the Great Smoky Mountains found on sample plot studies of the cove hardwoods.*

Those indicated by an asterisk are not known from the Southeastern States as Pre-Pleistocene fossils, but undoubtedly were there during the Tertiary, as shown by modern areas.

	Vernal aspect (10 stations)		Aestival aspect (9 stations)	
	Constancy %	Frequency %	Constancy %	Frequency %
*Rubus canadensis	50	12	89	18
Euonymus obovatus	40	21	44	23
*Parthenocissus quinquefolia	10	1	55	17
Viburnum lantanoides	10	1	33	9
Aristolochia macrophylla	30	5	11	2
Smilax hispida	.....	.....	33	3
Euonymus americanus	10	6	22	12
Hydrangea arborescens	10	1	22	5
Pyrularia pubera	10	1	11	1
*Sambucus pubens	20	2	.....	.....
Vitis aestivale	.....	.....	11	1
Rubus nigrobaceus	.....	.....	11	1
Grossularia Cynosbati	10	1	.....	.....

altogether, nine shrubs and four woody vines were found on the plots. These plants are never of very great importance (with respect to frequency, constancy, coverage, or density) in the cove hardwood forest type complex, except locally.

In studying the herbaceous layer, the Pteridophytes were sampled at the same time as the flowering herbs, but it was useful to separate them in presenting the results. Table 4 gives the data for the Pteridophytes. Only *Dryopteris intermedia, Athyrium thelypteroides,* and *Polystichum acrostichoides* were of sufficient constancy or frequency to be of much significance.

Table 5 lists all the flowering herbs encountered in the quadrat studies. They are grouped according to the constancy class to which they attain in either the vernal or the aestival aspect. For example, *Alsine tennesseensis* (conspicuously the most ubiquitous herbaceous species of the cove hardwood forest complex), *Tiarella cordifolia, Aster acuminatus,* and *Anemone quinquefolia* have a class V constancy in both aspects. *Erythronium americanum, Dentaria diphylla,* and *Viola sororia* reach class V in the spring flora, but not in the summer samples. The remaining species had a class V constancy only in the summer plots: *Urticastrum divaricatum, Viola blanda, Solidago Curtisii, Eupatorium urticaefolium,* and *Nabalus.* Such contrasts as are apparent between the vernal and the aestival samples are not all due to aspect, but are largely attributable to the heterogeneity of the herbaceous layer from station to station. Certain species of the spring flora, however, are usually absent from the summer stage, having completed their life-cycles by the time the full canopy of the forest has developed. In this group can

be mentioned *Erythronium americanum, Bicuculla canadensis, Bicuculla cucullaria, Claytonia virginica, Phacelia fimbriata,* and *Panax trifolium.* Species that are inconspicuous or have scarcely started their development in the spring, and which are of importance in the summer flora because of their high coverage, include such plants as *Eupatorium urticaefolium, Aster acuminatus, Urticastrum divaricatum, Solidago Curtisii, Monarda didyma, Impatiens pallida,* etc.

TABLE 4. *Pteridophytes of the Great Smoky Mountains found on sample plot studies of the cove hardwoods.*

Genera marked by an asterisk are not known from the Southeastern States as Pre-Pleistocene fossils, but from their modern areas they were undoubtedly in the region during the Tertiary:

	Vernal aspect (10 stations)		Aestival aspect (9 stations)	
	Constancy %	Frequency %	Constancy %	Frequency %
Dryopteris intermedia	90	36	89	77
Athyrium thelypteroides	60	20	100	45
*Polystichum acrostichoides	50	10	78	15
*Botrychium virginianum	40	5	44	10
Lycopodium lucidulum	40	9	33	13
Dryopteris noveboracense	10	6	55	32
*Botrychium dissectum	10	1	33	5
*Cystopteris fragilis	20	11	22	4
Athyrium asplenioides	.....	.....	22	5
*Botrychium obliquum	20	2	.....	.....
Dryopteris hexagonoptera	10	5	11	10
Athyrium pycnocarpon	.....	.....	11	3
Osmunda cinnamomea	.....	.....	11	2
Dryopteris marginalis	.....	.....	11	2
Dryopteris dilatata	.....	.....	11	1

The plants of the preceding tables are the ones that are considered later in the development of the thesis that the cove hardwood forest is an ancient forest of essentially Tertiary character. Bryophytic communities of the soil, tree trunks, etc., are not considered at this time. Any one wishing a more complete picture of the cove hardwood forests will find a discussion of the bryophytic communities by Cain and Sharp (1938).

THE TERTIARY CHARACTER OF THE COVE HARDWOOD FOREST

The method of ascertaining the ancient origin of most of the genera of the cove hardwood forest has already been discussed in the introduction. At this point, however, it is necessary to explain why generic units are used rather than species. In a study of Pleistocene plants of the Wicomico, Chowan, and Pamlico stages from North Carolina, Berry (1925b) found that none was foreign to the region as a whole, although several no longer exist at the localities where the fossils were found. Furthermore, only about

TABLE 5. *Species of the herbaceous stratum of the cove hardwood forest type complex of the Great Smoky Mountains National Park as observed from sample plot studies at 19 stations in the virgin forest.*

The vernal and aestival studies were made at different stations, so the differences are not wholly ones of aspect. Ten 1 sq. m. quadrats were used at each of the vernal stations; 10 6 sq.m. quadrats were used at each of the aestival stations. The species indicated by an asterisk are members of genera for which no evidence of their Tertiary nature is at hand. Nomenclature follows Small (1933).

Species are arranged according to the constancy classes to which they attain	Vernal flora		Aestival flora	
	Constancy %	Frequency %	Constancy %	Frequency %
Class V (81–100%)				
Alsine tennesseensis	100	99	100	100
Arythronium americanum	100	75	.....	.....
Tiarella cordifolia	100	73	89	81
Aster acuminatus	100	61	100	81
Dentaria diphylla	90	55	33	5
Anemone quinquefolia	90	54	100	38
Viola sororia	90	36	78	53
Urticastrum divaricatum	70	34	100	78
Viola blanda	80	59	100	72
Solidago Curtisii	70	39	100	62
Eupatorium urticaefolium	30	21	89	65
Nabalus sp.	60	16	89	33
Class IV (61–80%)				
Bicuculla canadensis	80	41	.....	.....
Viola hastata	80	35	11	8
Panax trifolium	80	35	.....	.....
Mitchella repens	80	24	67	37
Caulophyllum thalictroides	80	16	78	25
Claytonia virginica	70	61	.....	.....
Trillium erectum var. album	70	27	55	12
Cimicifuga americana	60	49	55	17
Oxalis montana	50	22	67	25
Ranunculus recurvatus	40	26	67	22
*Monarda didyma	30	12	67	12
Polygonatum biflorum	40	4	67	10
Class III (41–60%)				
Impatiens pallida	60	26	55	32
Poa cuspidata	60	21	33	14
Osmorrhiza Claytoni	60	16	55	22
Viola canadensis	50	13	11	4
Viola rostrata	50	12	11	1
Galium triflorum	.....	.....	55	29
Disporum lanuginosum	30	9	55	23
Carex flexuosa	.....	.....	55	13
Carex plantaginea	30	5	55	11
*Rudbeckia laciniata	30	12	44	20
Hepatica acuta	30	6	44	17
Tovara virginiana	.....	.....	44	12
*Hydrophyllum canadense	30	3	44	9
*Medeola virginiana	10	2	44	5
Class II (21–40%)				
*Phlox stolonifera	40	15	33	29
*Validallium tricoccum	40	11	33	10
Veratrum viride	30	18	.....	.....
Arisaema quinatum	30	14	33	9
Carex austro-caroliniana	30	11	22	3
Podophyllum peltatum	30	10	.....	.....

TABLE 5. (*Continued*)

Species are arranged according to the constancy classes to which they attain	Vernal flora		Aestival flora	
	Constancy %	Frequency %	Constancy %	Frequency %
Galium circaezans	30	7	.....	.....
*Xeniatrum umbellulatum	30	3	11	1
Cuscuta sp.	.....	.....	33	4
Arisaema triphyllum	10	1	33	4
Viola rotundifolia	20	8	33	3
*Chrosperma muscaetoxicum	.....	.....	22	13
Sedum ternatum	10	3	22	10
Cryptotaenia canadensis	.....	.....	22	9
*Adicea pumila	.....	.....	22	8
*Syndesmon thalictroides	.....	.....	22	5
Viola eriocarpa	.....	.....	22	4
*Campanulastrum americanum	.....	.....	22	3
Geum canadense	.....	.....	22	2
Peramium ophioides	.....	.....	22	2
Vagnera racemosa	20	3	22	2
CLASS I (1–20%)				
*Phacelia fimbriata	20	14	.....	.....
Viola pallens	20	9	.....	.....
Viola cucullata	20	8	.....	.....
Mitella diphylla	20	6	11	3
Geranium maculatum	20	6	11	2
*Zizia Bebbii	20	4	11	9
Lilium superbum	20	2	.....	.....
Juncoides bulbosum	20	2	.....	.....
Carex prasina	20	2	11	3
Trillium grandiflorum	10	10	11	3
Actea alba	10	6	.....	.....
Ranunculus fasicularis	10	4	.....	.....
Micranthes micranthidifolia	10	4	.....	.....
*Cymophyllus Fraseri	10	3	11	3
Juncoides saltuense	10	3	.....	.....
Galium aparine	10	2	.....	.....
Diphylleia cymosa	10	2	.....	.....
Ranunculus abortivus	10	1	11	2
*Collinsonia canadensis	10	1	.....	.....
Circaea latifolia	10	1	.....	.....
*Heucuera americana	10	1	11	1
Bicuculla cucullaria	10	1	.....	.....
Senecio Rugelii	10	1	.....	.....
Clintonia borealis	10	1	.....	.....
Glycine Apios	.....	.....	11	8
*Taenidia integerrima	.....	.....	11	5
*Blephilia hirsuta	.....	.....	11	5
Solidago axillaris	.....	.....	11	5
Hystrix Hystrix	.....	.....	11	3
*Houstonia purpurea	.....	.....	11	3
Meibomia nudiflora	.....	.....	11	2
Monotropa uniflora	.....	.....	11	1
Juncus tenuis	.....	.....	11	1
Thalictrum dioicum	.....	.....	11	1
Carex pennsylvanica	.....	.....	11	1
Panicum sp.	.....	.....	11	1
Carex stellata	.....	.....	11	1
Asclepias exaltata	.....	.....	11	1
Lysimachia quadrifolia	.....	.....	11	1

four per cent of the species are now extinct (a *Quercus* and a *Dendrium*). The remainder of the flora seems unchanged and includes such dry habitat plants as *Hicoria glabra, Quercus prinus, Q. velutina, Celtis occidentalis,* and *Vaccinium* (*Batodendron*) *arboreum.* Most of the plants are characteristic of moist to wet habitats and include *Taxodium distichum, Hicoria aquatica, Quercus palustris, Q. Michauxii, Planera aquatica,* and *Nyssa biflora.* The general practice of paleobotanists seems to be to consider Pleistocene fossils as conspecific with existing forms unless the weight of evidence is to the contrary. With older fossils, however, the opposite practice is the rule. One method that is very helpful in understanding the characteristics of a fossil flora is to indicate the nearest living relatives of the extinct forms. This can be illustrated by the following Miocene list from Berry (1916b), table 6. As far back as the Eocene, there was considerable resemblance

TABLE 6. *A comparison of species from the middle Miocene Calvert flora of Virginia and their closest living relatives.* (*From Berry 1916b*).

From the Calvert flora	Closest living relative
Salvinia formosa	Salvinia natans
Pinus sp.	Pinus taeda
Taxodium dubium	Taxodium distichum
Quercus calvertonensis	Quercus alba
Carpinus grandis	Carpinus caroliniana
Ulmus basicordata	Ulmus alata
Platanus aceroides	Platanus occidentalis
Cassia toraformis	Cassia Tora

between fossil species and modern ones. In the Wilcox flora (Berry 1930) *Cercis wilcoxiana* is very close to *C. canadensis,* and *Diospyros wilcoxiana* resembles *D. virginiana.* In the upper Eocene of the Claiborne and Jackson floras there are also examples of striking similarity between fossil and modern species (Berry 1924). Such pairs include *Hicoria jacksoniana* and *H. pecan, Castanea claibornensis* and *C. dentata,* and *Tilia jacksoniana* and *T. americana.* It is doubtful whether any species exist now that are very close to the Cretaceous floras. Certainly conspecific identity of types should be accepted only with great hesitancy, although many generic sections were established in the Cretaceous. It is apparent, then, that one could not get very far in proving the Tertiary nature of the modern flora of the Smokies by dealing with species.

On a basis of modern areas it would be possible to indicate that many of the cove hardwood species are of ancient origin. For example, in Europe and in eastern North America respectively there are many pairs of very closely related species such as *Oxalis Acetosella* and *O. montana, Polypodium vulgare* and *P. virginianum, Hepatica triloba* and *H. americana,* that have diverged only slightly. Between plants of eastern Asia and eastern

America for which geographic disjunction has been of long standing, there are some identities, and a striking series of very closely related pairs of species, such as *Caulophyllum robustum* and *C. thalictroides, Liriodendron chinense* (=*L. tulipifera* var. *chinense* Hemsl.) and *L. tulipifera,* etc. In other cases there is not a single pair of species, but a small group of closely related ones: *Pyrularia pubera* is represented by two species in the Himalayas, and *Buckleya distichophylla* (a semi-parasite on *Tsuga*) by three species in China and Japan. On this basis, however, it would not be possible to treat all the species of the cove hardwood forests because such close relatives are frequently absent.

Another difficulty, and a very serious one, with the method of geographic distribution applied to species lies in the necessity of critically examining published accounts and herbarium specimens from a taxonomic point of view. Such a procedure is beyond the scope of this paper. It seems sufficient to treat only of genera.

The study of the cove hardwood forests has been supplemented in one respect. Information has been brought together concerning the total arborescent flora of the Park. The genera native within the Park are listed in table 7, together with their fossil record in the southeastern states. This table also indicates those genera that were probably in the same region during the Tertiary, as shown by their modern areas explained above. Of the 67 genera, 36 are known from Cretaceous deposits of the southeastern states, 23 from the Eocene, 14 from the Miocene, and 10 from the Pliocene. From the whole Tertiary, there are records of 31 of these genera. Genera known from the Cretaceous of the region, but not discovered as yet in the Tertiary, were nevertheless probably still in the region during the Tertiary. These include *Strobus, Picea, Abies, Sabina, Populus, Liriodendron, Malus, Amelanchier, Crataegus, Acer, Rufacer, Sassafras, Benzoin, Cynoxylon, Kalmia,* and *Viburnum.* Altogether, the fossil records show that 46 genera of the arborescent flora of the Smokies were in the southeastern states in Pre-Pleistocene time.

Table 8 summarizes the data of table 7, and, according to the generic treatment of Small, it is seen that a total of 62 genera (93 per cent) date back to the Tertiary in this region. If the more conservative generic treatment found in Gray's Manual is used, the total of Tertiary genera is 96 per cent. Referring back to table 2, which summarizes the cove hardwood trees, we find that 90.5 per cent of the trees of the Aesculion are Tertiary, and that 84.6 per cent of those of the Tsugion are likewise that old. It is of special interest that all the trees that are dominant or codominant belong to genera that are of Tertiary character.

The summary for the flowering herbs (table 9) is especially interesting. Those species which have the highest constancy (Class V) are entirely of

TABLE 7. *Arborescent genera of the Great Smoky Mountains National Park, and their known occurrence as fossils in the southeastern United States during Cretaceous and Tertiary times.*

Genera	Cretaceous	Tertiary			Pleistocene	Pre-Pleistocene as indicated by modern areas
		Eocene	Miocene	Pliocene		
Pinus	x	.....	x	x	x	x
Strobus (Pinus)	x	.....	.....	.....	x	x (Bailey, 1933)
Picea	x	.....	.....	.....	x	x
Tsuga	.....	.....	.....	.....	.....	x
Abies	x	.....	.....	.....	.....	x
Sabina (Juniperus)	x	.....	.....	.....	x	x (Small, 1933)
Wallia (Juglans)	x	x	.....	.....	x	x (Small, 1933)
Hicoria (Carya)	.....	x	.....	x	x	x (Berry, 1923)
Populus	x	.....	.....	.....	x	x
Salix	x	x	x	.....	x	x
Carpinus	.....	.....	x	.....	x	x
Ostrya	.....	.....	.....	.....	x	x
Betula	x	.....	.....	x	x	x
Alnus	.....	.....	.....	.....	x	x
Fagus	x	.....	.....	x	x	x
Castanea	.....	x	.....	x	x	x
Quercus	x	x	x	x	x	x
Morus	.....	.....	.....	.....	x	x
Ulmus	.....	.....	x	.....	x	x
Celtis	x	x	.....	.....	x	x
Asimina	.....	x	.....	.....	x	.....
Tulipastrum (Magnolia)	.....	.....	.....	.....	.....	.....
Magnolia	x	x	.....	.....	x	x
Liriodendron	x	.....	.....	.....	x	x (Small, 1933)
Hamamelis	.....	.....	.....	.....	.....	x
Liquidambar	.....	x	.....	.....	x	x
Platanus	x	x	x	.....	x	x
Sorbus (Pyrus)	.....	.....	.....	.....	.....	x (Small, 1933)
Malus	x	.....	.....	.....	.....	x (Small, 1933)
Amelanchier	x	.....	.....	.....	x	x
Crataegus	x	.....	.....	.....	x	x
Prunus	x	x	.....	x	x	x
Padus (Prunus)	.....	.....	.....	.....	.....	x (Small, 1933)
Cercis	.....	x	.....	.....	x	x
Gleditsia	.....	x	.....	.....	x	x
Cladrastis	.....	x	.....	.....	.....	x
Robinia	.....	.....	.....	.....	x	.....
Rhus	x	.....	x	.....	.....	x
Ilex	x	x	x	x	x	x
Staphylea	.....	.....	.....	.....	.....	x
Aesculus	.....	.....	.....	.....	.....	x (Pax, 1928)
Acer	x	.....	.....	.....	x	x (Pax, 1926)
Saccharodendron (Acer)	.....	.....	.....	.....	x	..... (Pax, 1926)
Rufacer (Acer)	x	.....	.....	.....	x	x (Pax, 1926)
Negundo (Acer)	x	x	.....	.....	.....	x (Pax, 1926)
Rhamnus	x	x	x	.....	.....	x
Tilia	.....	x	.....	.....	x	x
Malachodendron (Stuartia)	.....	.....	.....	.....	.....	x
Sassafras	x	.....	.....	.....	.....	x (Small, 1933)
Benzoin	x	.....	.....	.....	x	x
Nyssa	x	x	x	x	x	x
Svida (Cornus)	x	x	.....	.....	x	.....
Cynoxylon (Cornus)	x	.....	.....	.....	.....	.....

TABLE 7 (*Continued*).

Genera	Cretaceous	Tertiary			Pleistocene	Pre-Pleistocene as indicated by modern areas
		Eocene	Miocene	Pliocene		
Aralia	x	x	.....	.....	.....	x
Clethra	.....	.....	.....	.....	x	x
Rhododendron	.....	.....	.....	.....	.....	x
Kalmia	x	.....	.....	.....	.....	x
Oxydendrum	.....	.....	.....	.....	.....	.....
Pieris (Andromeda)	x	.....	x	.....	.....	x (Small, 1933)
Batodendron (Vaccinium)	.....	.....	.....	.....	x	.....
Cyanococcus (Vaccinium)	.....	.....	x	.....	x	x
Diospyros	x	x	x	.....	.....	x
Halesia	.....	.....	.....	.....	.....	x
Fraxinus	x	x	x	x	x	x
Chionanthus	.....	.....	.....	.....	.....	x
Catalpa	.....	.....	.....	.....	.....	x
Viburnum	x	.....	.....	.....	x	x
Total genera 67	36	23	14	10	41	59

The records incorporated in the above table were obtained from the following publications:
CRETACEOUS: Berry (1914, 1919, 1921, 1923, 1925a, 1930), Knowlton (1919).
EOCENE: Berry (1924, 1930), Knowlton (1919).
MIOCENE: Berry (1923, 1916a, 1916b), Knowlton (1919).
PLIOCENE: Berry (1923), Knowlton (1919).
PLEISTOCENE: Berry (1923, 1925b), Hollick (1906), Knowlton (1919).
MODERN AREAS: From Dalla Torre and Harms (1900–1907) unless otherwise indicated; Bailey (1933), Berry (1923), Pax (1926, 1928), Small (1933).

Tertiary character. In the vernal aspect all the species that are over 40 per cent constant belong to genera that were present in the region during the Tertiary. The most striking feature of the table, however, seems to be the

TABLE 8. *Geological status of the arborescent genera of the Great Smoky Mountain National Park.*

	67 genera, according to Small (1933)		59 genera, according to Gray (1907)	
	No.	%	No.	%
Known from the Cretaceous of the Southeastern States	36	54	32	54
Known from the Tertiary of the Southeastern States	31	46	31	53
Known from Pre-Pleistocene of the Southeastern States	46	69	42	71
Known from the Pleistocene of the Southeastern States	43	64	39	66
Pre-Pleistocene, as indicated by modern generic areas	59	88	55	93
Total undoubtedly in the Southeastern States during Tertiary	62	93	57	96

TABLE 9. *The Tertiary character of the herbaceous stratum of the cove hardwood forest types of the Great Smoky Mountains National Park. Pteridophytes excluded.*

Constancy classes of the species (% of stands)	Vernal aspect (10 stations)		Aestival aspect (9 stations)		Total	
	Genera sampled	Per cent Tertiary	Genera sampled	Per cent Tertiary	Genera sampled	Per cent Tertiary
V (81–100%)	7	100	9	100	11	100
IV (61– 80%)	7	100	6	83	12	92
III (41– 60%)	4	100	10	70	12	75
II (21– 40%)	8	62	15	60	19	63
I (1– 20%)	21	76	20	70	34	76

Total number of genera = 76.
Total number of species = 98.

increase of the Tertiary percentage with an increase of constancy through classes II, III, IV, and V. This may be a coincidence, or it may indicate that the species of the more ancient genera are more thoroughly entrenched in these virgin communities than are the species of American endemic genera.

Finally, table 10 brings together the results for all the groups discussed.

TABLE 10. *Summary: Tertiary genera of the cove hardwood forest types of the Great Smoky Mountains National Park, based on sample plot studies at 31 stations in the virgin forest. Data based on Small's (1933) nomenclature.*

Classification	American endemic genera	Genera known from Pre-Pleistocene in Southeastern United States	Presumptive Tertiary genera from modern areas only	Total genera	Per cent of Tertiary genera
Trees					
All trees of the park	5	59	3	67	93
Cove Hardwood species sampled	3	20	5	28	89
Shrubs					
and woody vines	0	7	3	10	100
Herbs					
Ferns	0	4	3	7	100
Flowers	19	3	54	76	75
Totals					
Cove Hardwoods only	23	33	65	121	81[a]

[a] Using Gray's Manual names, the following higher percentages for Tertiary genera are obtained: All trees, 96; cove hardwood trees, 91; shrubs and woody vines, 100; ferns, 100; flowering herbs, 80; all cove hardwood genera, 86.

Using Small's generic designations, 93 per cent of all the arborescent genera of the Park undoubtedly go back to the Tertiary. For the cove hardwoods alone, we have the following results: 86 per cent of the tree genera, 100 per cent of the shrubs and woody vines, 100 per cent of the ferns, and 75 per cent of the flowering herbs are Tertiary. Of the 121 genera of all life-forms, 81 per cent are Tertiary. If Gray's Manual genera are used instead of

Small's, the Tertiary percentages are consistently higher, as indicated at the bottom of table 10. The percentage of endemism is conspicuously higher in the flowering herbs than in any other life-form.

It is not necessary to conclude that all American endemics not known from Cretaceous or Tertiary fossils are of recent origin. It is simply that there are no good means of ascertaining when these stocks arose.

The following paragraphs present more details concerning the geographic distributions of the genera under discussion. The following genera of trees have modern areas with a major disjunction, being present in eastern North America and Asia, and absent from Europe: *Tsuga, Hicoria, Magnolia, Liriodendron, Hamamelis, Liquidambar, Gleditsia, Cladrastis, Saccharodendron, Sassafras, Benzoin, Nyssa, Aralia, Pieris, Halesia, Chionanthus,* and *Catalpa.* To these 17 genera may be added, without taxonomic damage, *Malachodendron,* a finely drawn generic segregate of *Stuartia* (*Stewartia*) which occurs only in eastern North America and Japan. Also, according to Small, *Kalmia* consists of six North American species, but Dalla Torre and Harms recognize the genus also in western India.

A somewhat longer list of genera is typical of the northern hemisphere, principally in temperate regions, and they occur on the continents of America, Europe, and Asia. These genera belong in the same general group of ancient types as the above, but have not suffered as great a terrestrial disjunction. Included here are *Strobus, Pinus, Picea, Abies, Populus, Salix, Carpinus, Ostrya, Betula, Alnus, Fagus, Castanea, Quercus, Morus, Ulmus, Celtis, Platanus, Sorbus, Malus, Amelanchier, Crataegus, Prunus, Padus, Cercis, Rhus, Ilex, Staphylea, Acer, Rufacer, Negundo, Rhamnus, Tilia, Clethra, Rhododendron, Cyanococcus, Diospyros, Fraxinus, Catalpa,* and *Viburnum.* Again without serious taxonomic damage, to these 39 genera can be added *Sabina,* an American segregate of *Juniperus, Wallia,* an American segregate of *Juglans,* and *Svida* and *Cynoxylon,* American segregates of *Cornus.*

This leaves *Asimina, Tulipastrum, Robinia, Oxydendrum,* and *Batodendron* as American endemics. Of these, *Asimina* is known from the Eocene and Pleistocene of the southeastern United States, *Robinia* from the Miocene elsewhere, and *Batodendron* from the Pleistocene of the southeastern United States.

A survey of the herbaceous flowering-plant genera shows the following to have the typical American-Asian disjunction, being absent from Europe, and frequently from western Asia and western America: *Tiarella, Urticastrum, Bicuculla, Panax, Mitchella, Caulophyllum, Claytonia, Trillium, Osmorrhiza, Disporum, Tovara, Arisaema, Podophyllum, Vagnera, Mitella, Diphylleia, Clintonia, Glycine, Hystrix, Meibomia,* and *Monotropa.*

To these 21 genera can be added 36 more that have a circumboreal distri-

bution which was undoubtedly attained in Pre-Pleistocene time: *Alsine, Erythronium, Aster, Dentaria, Anemone, Viola, Solidago, Eupatorium, Nabalus, Cimicifuga, Oxalis, Ranunculus, Polygonatum, Impatiens, Poa, Galium, Carex, Hepatica, Veratrum, Cuscuta, Sedum, Cryptotaenia, Geum, Peramium, Geranium, Lilium, Juncoides, Actea, Micranthes, Circaea, Senecio, Juncus, Thalictrum, Panicum, Asclepias,* and *Lysimachia.*

According to the information at hand, the following 19 genera are American endemics, not having either the trans-Atlantic or the trans-Pacific disjunction: *Monarda, Rudbeckia, Hydrophyllum, Medeola, Phlox, Validallium, Xeniatrum, Chrosperma, Adicea, Syndesmon, Campanulastrum, Phacelia, Zizia, Cymophyllus, Collinsonia, Heuchera, Taenidia, Blephilia,* and *Houstonia.* This list is somewhat longer, being based on Small (1933) and the recognition of certain segregate genera, than if the genera accepted by Dalla Torre and Harms and Gray are used. For example, *Validallium* is a segregate of *Allium, Adicea* of *Pilea, Syndesmon* of *Anemone, Campanulastrum* of *Campanula,* and *Cymophyllus* of *Carex.* Furthermore, *Phlox* is strictly American except for one species that extends from Alaska into Siberia and may have attained its range relatively recently.

DISCUSSION

The so-called Arctotertiary vegetation is known to have extended from Greenland over northern Europe to the northern Urals. It extended also from the middle zone of Asia to Manchuria, Sachalin and northern Japan. In North America it is known to have occurred from Alaska to the Pacific Northwest, and in the Atlantic Northeast. The vegetation of this wide region consisted of deciduous, summergreen trees (mesophanerophytes) with an admixture of evergreen conifers. It probably required a mean annual temperature of about 10° C. The more important genera of the forest include *Fagus, Castanea, Ulmus, Alnus, Betula, Corylus, Populus, Juglans, Carpinus, Liquidambar, Sequoia,* and *Ginkgo.* Although herbaceous fossils are almost non-existent, except for a few aquatics, there are excellent reasons for believing that the deciduous broad-leaved forests had a well developed herbaceous layer very similar to that of today.

The most illuminating and complete study of this problem is by Lippmaa (1938) on the *Galeobdolon-Asperula-Asarum*-Union of Europe. This herbaceous union is composed of plants of the hemicryptophytic and cryptophytic life-forms and requires relatively strong shade in summer, light in springtime during the flowering period, and a mild humus such as is formed under deciduous forest. Lippmaa concluded that it was no chance that the area of the *Galeobdolon*-Union and its relative societies corresponds so well with the area of the temperate Tertiary forests. The herbaceous vegetation undoubtedly has had the same history as the mesophanerophytes, except that

in Europe the tree vegetation suffered more than the herbs during the glacial period. The area of the *Galeobdolon*-Union and its counterparts must have been as wide in the Tertiary as that of the forest formation with which it is associated.

Lippmaa makes use of detailed analyses of the taxonomic relationships of the character and constant species of the *Galeobdolon*-Union, and of their present distributional patterns. He reached the following conclusions: "All character-species and constant-species of the *Galeobdolon-Asperula-Asarum*-Union are ancient forest plants which are often of an isolated systematic position and whose relatives dwell all over Eastern Asia, North America, the Himalayas, and in part in the Caucasus and southern Europe. Several of the species are relic plants occurring in smaller regions separated from the modern main distribution (*Asperula odorata, Actea spicata, Sanicula europaea, Stellaria holstea, Asarum europaeum, Bromus Beneckenii, Carex digitata*). The species of the union already existed in the Tertiary or they were represented by species which today are very closely related. . . . In Eastern Asia and North America plant unions exist which stand very close to the *Galeobdolon-Asperula-Arisaema*-Union; floristically, however, the species list is wholly different. Only single widely distributed species such as *Aruncus silvester* occur as floristic 'binders.' On the other hand there is undoubtedly a very far-reaching agreement with regard to the elementary life-form which is this union's own. So, for example, in all the named unions, the *Anemone* life-form plays a very important role (*Majanthemum, Anemone, Paris, Dentaria, Trientalis, Trillium* species)."

It seems reasonable to conclude, from all the evidence that has been presented, even without data concerning species, that the virgin hardwood forests of the Great Smoky Mountains National Park are the finest example of temperate Tertiary forests to be found anywhere in the world, except probably in Eastern Asia. This much is certainly true, a botanist familiar with the modern flora of the cove hardwood forests of the Smokies would find himself "at home" among the temperate forests of the Miocene and later Tertiary, could he be transported back in time. The principal difference would be in the presence in the forest of such temperate trees as *Sequoia* and *Ginkgo*, now very restricted.

SUMMARY

1. An extensive list of species of Angiosperms and Pteridophytes of the virgin cove hardwood forests of the Great Smoky Mountains National Park was obtained from sample plot studies at 31 stations. This was supplemented by a complete list of the trees of the Park.

2. From publications on paleobotany it was found that 27 per cent of

the 121 genera (mostly woody plants) are known as fossils from Cretaceous and Tertiary deposits of the southeastern states.

3. In addition to those genera known to have been in the southeastern states during Pre-Pleistocene time, 54 per cent are probably as ancient as the middle or late Tertiary as shown by their modern areas.

4. A break-down of the totals reveals the following percentages of Tertiary genera:

a. All trees of the Park, 93 per cent of 67 genera;
b. Cove hardwood trees sampled, 86 per cent of 28 genera;
c. Cove hardwood shrubs sampled, 100 per cent of 10 genera;
d. Cove hardwood ferns sampled, 100 per cent of 7 genera;
e. Cove hardwood flowering herbs sampled, 75 per cent of 76 genera;
f. All cove hardwood species sampled, 81 per cent of 121 genera.

5. Species of most importance in the cove hardwood forests are almost exclusively members of genera of ancient origin. The forest dominants are exclusively of ancient origin.

6. Species of American endemic genera are seldom of high constancy, frequency, or coverage in the cove hardwood forests.

7. It is not known whether the Great Smoky Mountains flora is richer in ancient plant species than other North Temperate regions, because comparable data are not available, but all evidence indicates that the cove hardwood forests of the Southern Appalachians, which have their maximum development in the Smokies, are very similar to the rich, mesophytic, and once circumboreal Arcotertiary forests.

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A POLLEN STUDY OF TWO BOGS ON ORCAS ISLAND, OF THE SAN JUAN ISLANDS, WASHINGTON[1]

HENRY P. HANSEN

INTRODUCTION

The San Juan Islands lie between the mainland of the state of Washington and the southern end of Vancouver Island, about 75 miles from the Pacific Ocean through the Strait of Juan de Fuca. Orcas Island is one of the largest and most northern of the group. It is about 11 miles in extent from east to west, and about 9 miles from north to south. The highest point is Mt. Constitution with an elevation of about 2400 feet. The San Juan Islands were glaciated during the Pleistocene (Bretz 1913), and the higher areas are rocky with little soil. Lower areas near sea level are covered with glacial drift and glacio-lacustrine and glacio-fluviatile deposits. The climate of the San Juan Islands is mild and somewhat drier than that of the Puget Lowland to the east and south. The mean annual precipitation at Olga, at the southern tip of Orcas Island, is about 29.5 inches, and at the north end of East Sound it is slightly over 30 inches. (Climatic Summary, U. S. D. A., 1936.) At San Juan, on San Juan Island, a few miles to the west and south, the mean annual precipitation is about 22.5 inches, while at Anacortes on the mainland to the southeast it is about 27 inches. About 15 per cent of the precipitation occurs during the growing season. In some areas the porosity of the soil permits rapid drainage, whereas in others the absence of much soil results in rapid run-off. The prevailing winds are from the west.

LOCATION AND CHARACTERISTICS OF THE BOGS

One of the bogs is located near the summit of Mt. Constitution on the northeastern part of the island, while the other is situated near sea level at the southern end of the island. There are several bogs on Mt. Constitution, one of which has been described by Rigg and Richardson (1934). The one of this study is several acres in extent and is covered largely with sedge (*Carex* spp. and *Cyperus* sp.) and Labrador tea (*Ledum groenlandicum*). Other of the more common plants are hardhack (*Spiraea douglasii*), salal (*Gaultheria shallon*), cottongrass (*Eriophorum chamissonis*), sundew (*Drosera rotundifolia*), and twinflower (*Linnaea borealis americana*). Trees on the bog in their apparent order of invasion are lodgepole pine (*Pinus contorta*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*), the first being the most abundant.

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The lowland bog is situated at the west end of Killebrew Lake, about three-quarters mile north of Grindstone Bay, and about 10 miles southwest of Mt. Constitution. The lake supports various stages of hydrarch plant succession, including submerged, floating, and cattail-bulrush associes. On the bog grow purple marshlocks (*Potentilla palustris*), buckbean (*Menyanthes trifoliata*), spike-rush (*Eleocharis acicularis*), and *Dulichium arundinaceum*. Many other species of bog and marsh plants are present, but those mentioned seem to be characteristic of the associes.

Peat samples were obtained at quarter-meter intervals with a Hiller peat borer. The depth of the Mt. Constitution bog is 9 meters in the area of sampling, and the Killebrew Lake bog is 9.5 meters deep. A stratum of volcanic ash occurs between 7 and 7.5 meters in the montane bog, and at 7 meters in the lowland bog. Ash fragments are scattered throughout a half-meter thickness of peat, but are most abundant at these levels. The relative stratigraphic position of the ash layers is similar to that of most peat profiles in northern Washington, suggesting that the source of the ash was the same volcanic action. According to geologists, the most probable source is Glacier Peak in the Cascades of northern Washington.

In the Mt. Constitution bog, fibrous peat occurs close to the bottom underlain by only a thin stratum of sand and silt resting directly on bedrock. This denotes that the proximity of the original pond to the summit of the mountain prevented the erosion of considerable sand and silt into it, which is often the case in Pacific Northwest bogs. The presence of pollen in these lowest levels, however, indicates that forest invasion of adjacent areas began soon after glacial retreat. The Killebrew Lake bog has a much greater thickness of silt and clay underlying the organic peat. In preparation of the peat for microscopic analysis, the potassium hydrate method was employed. From 100 to 200 pollen grains were identified from each horizon. In identification of the winged conifer pollen, the size range method was used (Hansen 1941a, 1941b, 1941c). The tables showing the percentages of conifer pollen and the number of non-significant pollen grains of herbs, grasses, and deciduous trees are omitted because of the unusual scarcity of the latter. Those species recorded as 1.5 per cent or less are shown on the diagram as 1 per cent.

FORESTS OF THE SAN JUAN ISLANDS

The San Juan Islands lie within the hemlock–cedar climax formation of the Coast Forest (Weaver & Clements 1938). Certain factors of the environment, however, are apparently unfavorable for western hemlock and western red cedar (*Thuja plicata*) to thrive as the principal dominants. These islands are also within the Humid Transition life area (Piper 1906). Forest type maps (1936) show that the San Juan Islands are forested largely with second-growth Douglas fir and subalpine and noncommercial types. Mt. Con-

stitution is forested chiefly with lodgepole pine (*Pinus contorta*), with some Douglas fir (*Pseudotsuga taxifolia*) and western hemlock, and scattered specimens of western white pine (*Pinus monticola*) and lowland white fir (*Abies grandis*). The hills adjacent to the Killebrew Lake bog are forested with second-growth Douglas fir, and some hemlock, lowland white fir, western red cedar, Sitka spruce, and western white pine. The most common broadleaf species are largeleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and cottonwood (*Populus trichocarpa*). In dry exposed areas on the south slopes, Oregon white oak (*Quercus garryana*) occurs, while the presence of prickly pear (*Opuntia fragilis*) reflects the dryness of the summers.

In the hemlock–cedar formation of the Puget Lowland of western Washington, Douglas fir persists as subclimax and the chief dominant because of recurring fire during the past (Munger 1940). Over much of the area designated as being forested with this association, however, the environment is unfavorable for hemlock and cedar. In some of these areas Douglas fir thrives as the chief dominant even though fire does not occur. It is suggested that the climate is too dry for hemlock to supplant Douglas fir in the course of normal, uninterrupted forest succession (Munger 1940). The east slope of the Coast Range and the Willamette Valley of western Oregon are examples of such regions. Not only is hemlock practically absent at the present time, but pollen profiles from these areas reveal that hemlock has played only a minor role during all or most of the post-Pleistocene (Hansen 1941a, 1942a). Insufficient rainfall is perhaps the main factor inhibiting hemlock from superseding Douglas fir, even in the absence of fire, but the edaphic and topographic conditions may also exercise some control. The annual precipitation in the Willamette Valley is greater than in parts of the Puget Sound region, where hemlock does replace Douglas fir in normal forest succession. The summer precipitation, however, is slightly less and may be the limiting factor in preventing hemlock from invading and assuming predominance. A lower humidity and greater amount of evaporation during the growing season may also be contributing factors. On Orcas Island, then, it seems probable that the annual rainfall, which is slightly less than in the Puget Sound region, and the dry summers are responsible for the comparative absence of hemlock from the forest complex. On the higher parts of the island, the rocky terrain is undoubtedly an additional factor instrumental in its scarcity.

POSTGLACIAL FOREST SUCCESSION

In both areas lodgepole pine was the predominant species when the lowest pollen-bearing sediments were deposited. In the montane bog it is recorded as 71 per cent (fig. 1), and in the Killebrew Lake bog as 69 per cent (fig. 2). The initial postglacial invasion of lodgepole pine in these areas is

consistent with that of many other regions of the Pacific Northwest (Hansen 1938, 1939a, 1939b, 1940a, 1940b, 1941a, 1942a). The trend of lodgepole pine is very different in the two profiles. In the Mt. Constitution bog, lodgepole pine increases from the bottom to 90 per cent at 8 meters, the highest proportion to which it is recorded in any bog thus far studied. It shows a general decrease from this maximum to the surface, fluctuating between 85 per cent at 7.25 meters and 44 per cent at 1 meter, its lowest proportion of the profile. It then increases to 60 per cent at the top. In the Killebrew Lake profile, lodgepole pine diminishes sharply from the bottom to only 7 per cent at 6.5 meters, and from this horizon upward, it fluctuates between 12 and 4 per cent. It is recorded as 6 per cent at the surface. Western white pine is next most abundantly represented, at the bottom and is recorded as 20 and 15 per cent in the montane and lowland bogs respectively (figs. 1, 2). In the Puget Lowland of western Washington, white pine was also one of the predominant pioneer invaders. It diminishes slightly upward from the bottom, but it remains generally constant throughout both profiles, fluctuating between 12 and 1 per cent in the montane bog, and 14 and 1 per cent in the other.

Douglas fir also differs in its successional trends as recorded in the two profiles. In the Mt. Constitution bog, it is recorded as 3 per cent at the bottom, and fluctuates between this and nothing to 6.5 meters (fig. 1). It is then recorded as slowly increasing upward in the profile, reaching its maximum proportion of 30 per cent at 1 meter, and then declining to 15 per cent at the top. In the Killebrew bog, Douglas fir is recorded as 7 per cent at the lowest level, and then increases sharply to its maximum of 67 per cent at 5 meters (fig. 2). It shows a slight decline from this horizon to the surface, where it is represented by 52 per cent of the conifer pollen present.

In the montane bog, western hemlock exhibits somewhat the same general trend as Douglas fir, but it does not reach such high proportions as low in the profile (fig. 1). Its maximum is 30 per cent at 2 meters, and it then diminishes to 17 per cent at the uppermost level. In the lowland bog, hemlock is recorded more abundantly, as is Douglas fir (fig. 2). It increases lower in the profile and attains proportions of 20 per cent at 7.5, 6.5, 4.75, and 3.75 meters, and then declines and remains constant to the top where it is represented by 14 per cent. This species does not reach higher proportions in the Killebrew bog, but it is more consistently represented by greater proportions throughout the profile than in the montane bog.

Other forest trees recorded in appreciable proportions are Sitka spruce and fir. Spruce is represented more abundantly and consistently in the lowland bog (figs. 1, 2). Here its greatest proportion is 9 per cent at the bottom; in the montane bog it attains 7 per cent at 7 meters. This is consistent, because spruce thrives better near the ocean than at higher elevations farther

inland. Fir pollen is listed under the genus only, since the pollen of all species except lowland white fir is only sporadically present. The other species whose pollen was noted are noble fir (*Abies nobilis*), silver fir (*A. amabilis*), and alpine fir (*A. lasiocarpa*). None of these species was noted on Orcas Island, although they may have existed there in the past. Possible sources of their pollen are the other San Juan Islands, Vancouver Island, or the Olympic Peninsula, because of the prevailing westerly winds. Silver and alpine fir are common in the Olympic Mountains, but the occurrence of noble

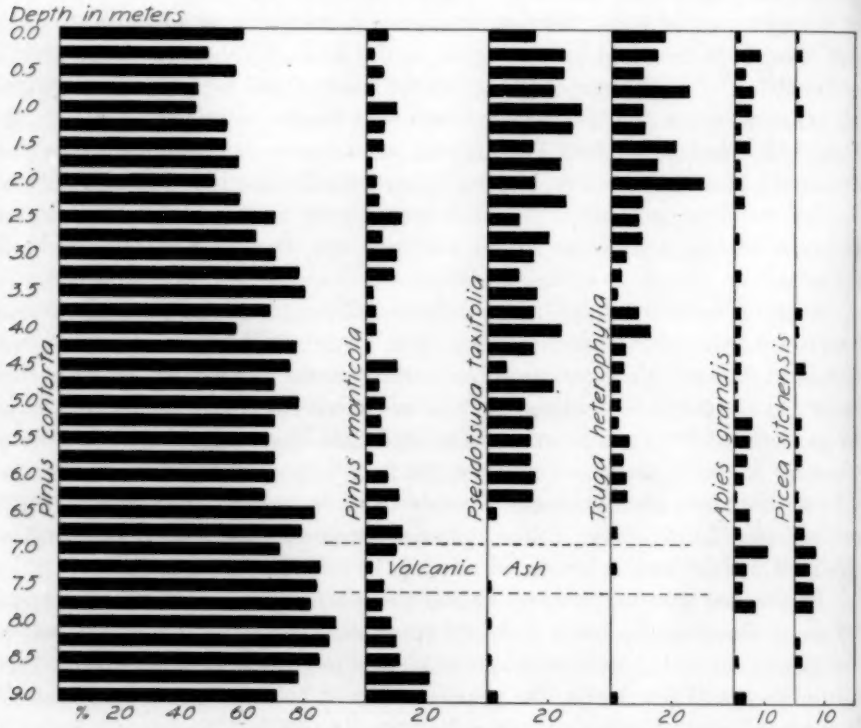

FIG. 1. Pollen profiles. Mt. Constitution bog.

fir is not certain. Noble fir was reported by Sudworth (1908), but Jones (1936) in an extensive study of the flora of the Olympic Peninsula, was unable to find it. This does not exclude the possibility of its existence in the past, and pollen of this species was present in the upper levels of the profiles. A pollen study of a bog on the west side of the Olympic Peninsula also reveals the presence of noble fir pollen, but not in the uppermost level (Hansen 1941d). Fir pollen is more consistently abundant in the Killebrew Lake bog, which is logical because lowland white fir thrives best in low, damp areas. The greatest proportion attained by fir pollen is 16 per cent at 7.25 meters

and at the surface in the lowland bog (fig. 2), whereas in the montane peat deposit it reaches a maximum of 11 per cent at 7 meters and is not present at all horizons (fig. 1). Mountain hemlock (*Tsuga mertensiana*) is sporadically represented in both profiles. Pollen of this species may have come from Vancouver Island or the Olympic Mountains, although it also may have

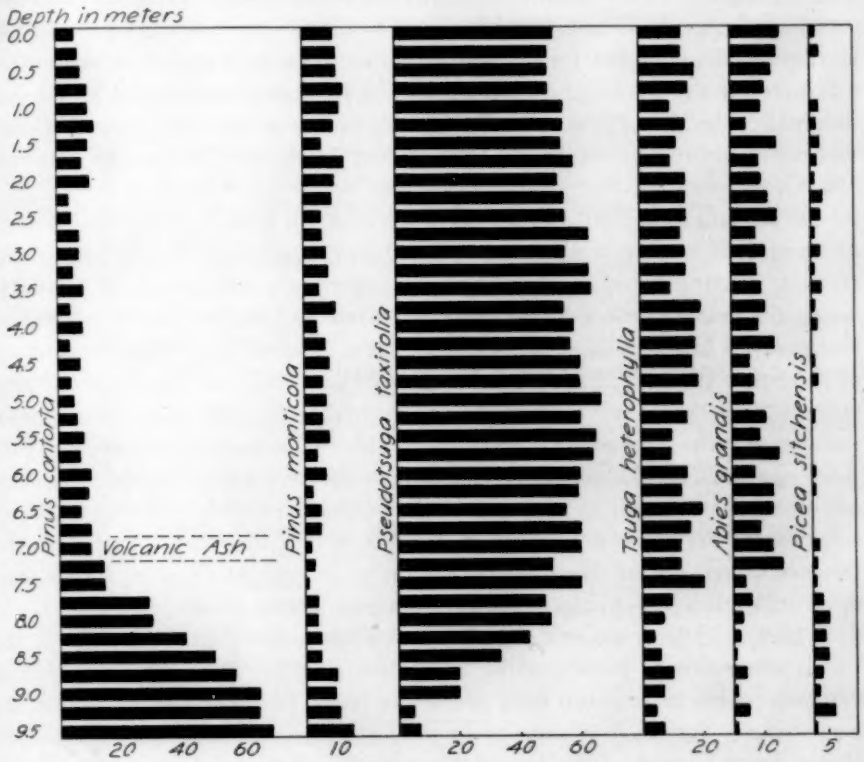

FIG. 2. Pollen profiles. Lake Killebrew bog.

existed in the San Juan Islands earlier in post-Pleistocene time. Broadleaf trees represented by their pollen are red alder and largeleaf maple, both of which are more abundantly recorded in the Killebrew Lake bog. Sedge pollen increases and yellow pondlily pollen diminishes in abundance upward in both profiles, marking the progress of hydrarch plant succession in the bog.

INTERPRETATION OF THE POLLEN PROFILES

The trend of postglacial forest succession in the lowland area of Orcas Island, as portrayed by the pollen profiles of the Killebrew Lake bog, is somewhat similar to that of the Puget Sound region (Hansen 1938, 1940a, 1941a). Pollen analyses of peat deposits there reveal that lodgepole pine was the pioneer postglacial invader and was rapidly supplanted by Douglas fir.

Western hemlock increased more gradually than Douglas fir, but eventually superseded the latter and remained slightly predominant until the advent of white man. In areas adjacent to Killebrew Lake, however, hemlock was never so abundant as in the Puget Sound region, and Douglas fir has maintained a wide degree of predominance since it superseded lodgepole pine. This substantiates the theory that the lack of moisture, particularly in dry summers, on Orcas Island, has prevented hemlock from reaching proportions similar to those in the Puget Sound region. The importance of abundant moisture for the development of hemlock is further corroborated by its predominance in post-Pleistocene forest succession along the Oregon Coast, where the annual precipitation varies from 70 to over 100 inches (Hansen 1941c).

On the summit of Mt. Constitution the thin soil mantle has probably been as important as moisture in controlling forest succession. In fact the rocky terrain, causing rapid run-off, tends to accentuate the dearth of available water for tree growth. Glacial scour left little soil and only a thin layer of residual soil has developed since deglaciation. The much greater intolerance of lodgepole pine for shade than Douglas fir and hemlock, has been compensated for by the edaphic conditions unfavorable for the latter two species. Lodgepole pine has consequently been able to successfully compete with these species. That lodgepole pine is able to thrive under edaphic conditions adverse for other species is shown by its pioneer invasion of areas formerly covered by Pleistocene glaciers in Washington, young sand dunes on the Oregon Coast, climax bogs, pumice mantles in central Oregon, burns, and other edaphically disturbed regions (Hansen 1941c, 1942b, 1942c).

There is little or no evidence for post-Pleistocene climatic trends in the forest succession as portrayed by the pollen profiles. The low proportion of hemlock pollen throughout both profiles in itself, however, denote that it has been too dry for its development to predominance, such as occurred in the Puget Sound region. The rather local representation of the surrounding forests in each respective bog, raises the question as to the size of an area that is represented by its tree pollen in a bog. The small size of the island, restricting the source of the pollen, may tend to accentuate this degree of localization.

SUMMARY

Pollen analyses of two peat deposits on Orcas Island, Washington, reveal different trends of post-Pleistocene forest succession in their respective adjacent areas. In both bogs, lodgepole pine is recorded as having been the predominant, pioneer, postglacial invader. In areas surrounding the montane bog, lodgepole pine maintained predominance throughout the postglacial period to the present. The existing forests are composed chiefly of lodgepole pine. In areas adjacent to the other bog, near sea level, lodgepole

pine was early replaced by Douglas fir which remained predominant during the rest of the post-Pleistocene. The San Juan Islands are located within the hemlock–cedar climax, but hemlock neither superseded nor became nearly so abundant as Douglas fir during the postglacial. This was probably due to the low summer precipitation and the unfavorable edaphic conditions for hemlock. There is little evidence for climatic trends, and it is probable that the ocean has served to maintain an equable climate during postglacial time.

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PHYTOPHTHORA ROT OF BELLADONNA[1]

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INTRODUCTION

With the increasing trend toward the cultivation of pharmaceutical crops, a number of interesting plants and their diseases are encountered. One of the crops recently brought into cultivation again in southern California is belladonna, *Atropa belladonna* L. Of the diseases observed on this host, rot, principally of the root and stem, caused by *Phytophthora parasitica* Dastur, is the most important.

Plantings of belladonna in southern California are confined to small plots, usually from 1 to 10 acres; they are generally coastal and are to be found growing on a number of different soil types. On the heavy, poorly drained soils, root-rot is an important and often limiting factor in growth; on the lighter, adequately drained soils, it is rarely observed and is of little concern.

REVIEW OF LITERATURE

The first record of a root-rot of *Atropa belladonna* is apparently from England, where Barker (1917–1918) reports a *Phytophthora* sp. to be responsible. Westerdijk and van Luijk (1920) later describe a root-rot of belladonna in the Netherlands and state that *P. erythroseptica* Pethyb. is the causal agent. Alcock (1926) records the occurrence of a stem-rot and wilt of belladonna in Scotland and attributes the trouble to *P. erythroseptica* var. *atropae* Alcock. Tucker (1931) does not consider this varietal segregation valid, however, and states that "the reasons for separating the Atropa strain are not very convincing, and, pending further evidence, the writer prefers to include it in *P. erythroseptica.*"

Other organisms attack belladonna and cause effects which may be mistaken for those of *Phytophthora* spp. Parisi (1921) reports that *Thielavia basicola* Zopf[2] attacks belladonna in Italy, but adds that infected seedlings recover when planted in the open field in well-aerated soil. MacMillan (1941) reports damping-off of this host, due to *Rhizoctonia* sp. and to *T. basicola,* in California, and describes a root-rot attributed to *Fusarium* sp.; he states that the "mycelium of *Fusarium* is usually found. . . ." No inoculations are recorded.

A preliminary description of the root-rot caused by *Phytophthora* is

[1] Paper No. 478, University of California Citrus Experiment Station, Riverside, California.

[2] Probably *Thielaviopsis basicola* (Berk.) Ferraris, according to McCormick (1925, p. 551).

given by the author (1941) in a short article dealing with several diseases of belladonna in California.

SYMPTOMS OF THE DISEASE

The disease affects fibrous and fleshy roots, crowns, stems, and, to a lesser extent, leaves of the plant. The fungus attacks both fine and larger fibrous roots and causes brown, discolored areas which are at first firm but later become watersoaked and flaccid and subsequently die (fig. 1). The fleshy portion of the root is frequently parasitized; it subsequently turns dark brown to black in color and becomes watersoaked and flaccid. Sunken, necrotic, longitudinally oriented areas, which progress upward into the stem, are often discernible on the outside of the exposed fleshy part of the root (fig. 2).

As root infection progresses upward, other roots and often the crowns of the plants are attacked; incipient shoots that are affected turn dark and die. Frequently the roots of a plant may be badly damaged while the crown remains fairly intact and sends out new shoots; such plants may recover but are of little commercial value. Plants with naturally infected crowns invariably die, being unable to produce new roots; the shoots, becoming infected, turn brown and rot. Sometimes crowns become infected first, and the infection progresses downward to the root and upward into the stem.

Conspicuous, dark, slightly sunken necrotic areas are produced on infected stems. Stems so infected frequently show signs of wilting, the leaves turn yellow, and the plant eventually dies.

Often plants which lack vigor, characterized by yellowed leaves and by some signs of wilting, will show no signs of stem infection. But when such plants are dug and the soil is carefully washed away from the roots, only a few badly infected and discolored roots are found. Sometimes plants are observed to have an abnormally large number of sparsely foliated, slender shoots; the roots and crowns of such plants have also been found to be badly diseased.

Along the coast, under conditions of high relative humidity and warm air temperatures prevalent during the summer months and usually following a foggy period, young shoots and leaves of the plants are attacked, the affected parts collapsing on becoming watersoaked. Through leaf and stem infections the disease may spread throughout the planting.

THE CAUSAL ORGANISM

Phytophthora parasitica was readily obtained in pure culture when tissue plantings of bits of diseased material from the margin of necrotic areas, or from fairly recently infected roots of belladonna plants, were made on cornmeal agar and on plain water agar. The fungus was identified by Dr.

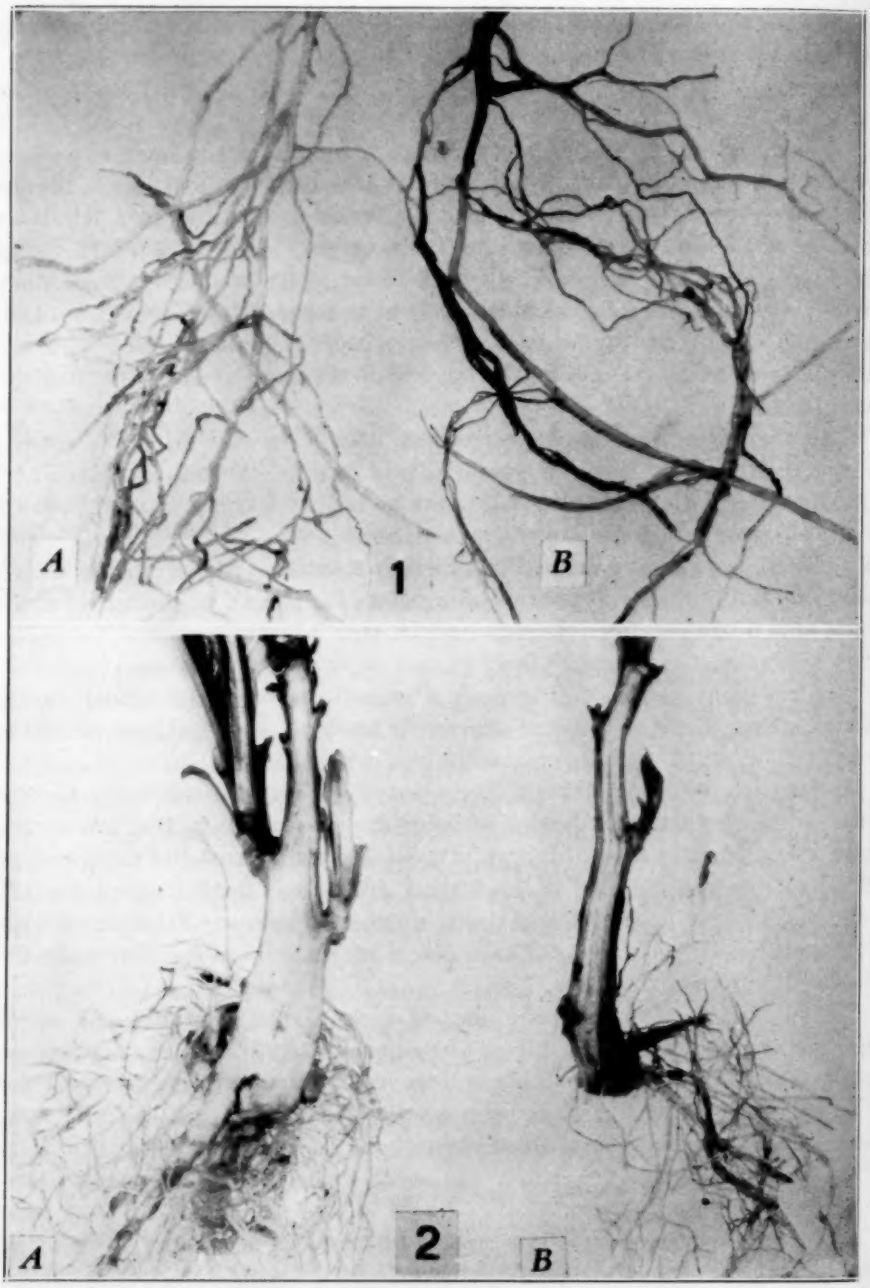

FIG. 1. Phytophthora rot of belladonna: A, noninoculated control; B, symptoms produced on fibrous roots by *Phytophthora parasitica* 16 days after inoculation in the greenhouse. In addition to the discolored areas on the roots, note the smaller number of roots on the infected plant. FIG. 2. Phytophthora rot of belladonna: A, noninoculated control; B, symptoms produced on roots and stem by *Phytophthora parasitica* 27 days after inoculation in the greenhouse. The lesion is dark, slightly sunken, and vertically disposed. Note the paucity of roots and the relative size of the shoots in B, as compared with A.

C. M. Tucker. Isolations were typical of the species. *Fusarium* spp. were sometimes obtained in conjunction with *P. parasitica* when infected tissue was taken from badly diseased portions of the plant and plated on these media.

Sporangia of the fungus are typically acrogenous, are infrequently intercalary or borne laterally, and are ovate with a prominent apical papilla; they measure 23.6–49.8 μ by 21.1–36.5 μ, the mean 37.6 μ by 31.0 μ. Oögonia are acrogenous, intercalary or borne terminally on short lateral branches, and from spherical to slightly obovoid, with a smooth wall; in diameter, they measure 19.2–24.9 μ, the mean 22.6 μ. Antheridia are amphigynous. Oöspores are thick-walled and smooth and largely fill the oögonial cavity; they measure 16.3–21.2 μ, the mean 20.1 μ, in diameter.

The cardinal temperatures for growth are: minimum, 10° C; optimum, 30–32.5°; and maximum, 37.5°.

These observations on morphology and temperature-growth relations are in conformity with those reported by Tucker (1931).

PATHOGENICITY

Cuttings originally rooted in a mixture of sterile soil and sand were transplanted to 6-inch pots containing sterile potting soil, in the greenhouse. Pure cultures of the fungus, grown on a mixture of sterilized whole oats and wheat, were added to the soil of one lot of 50 plants; sterile oats and wheat, only, were added to another lot of 10 plants. After 14–16 days, a few plants in pots infested with the fungus ceased growing and assumed a yellowed appearance. Twenty days after inoculation, all the fungus-inoculated plants had stopped growth, had become yellow, and showed signs of wilting (fig. 3); stem lesions became visible 23 days after inoculation. Plants grown in pots which received only the sterile-grain mixture remained healthy and continued to grow. When the affected plants were removed from their pots and the soil was carefully washed away from the roots, lesions such as those observed on naturally infected plants were found in abundance. Isolations made from artificially infected stems and roots proved pathogenic upon reinoculation and produced symptoms indistinguishable from those caused by natural infection.

This same procedure was employed with plant material derived from seed sown in sterile soil; the results were similar to those already described.

Cultures of *Fusarium* spp., isolated together with *Phytophthora parasitica* from diseased material, were grown on the sterile-grain medium. This inoculum was added to sterile soil in 6-inch pots containing belladonna plants, according to the procedure outlined above. No visible symptoms of disease were observed after one month. Plants receiving this treatment were taken from their pots, and the soil was removed by washing in water; no

root necrosis was observed. It is concluded that the *Fusarium* spp. used in this test were not pathogenic to belladonna and did not contribute to the root-rot problem.

Belladonna plants have been observed to damp-off. The fungi concerned are usually *Pythium debaryanum* Hesse, *P. irregulare* Buis., and *P. ultimum* Trow, though occasionally *Phytophthora parasitica* has been isolated from

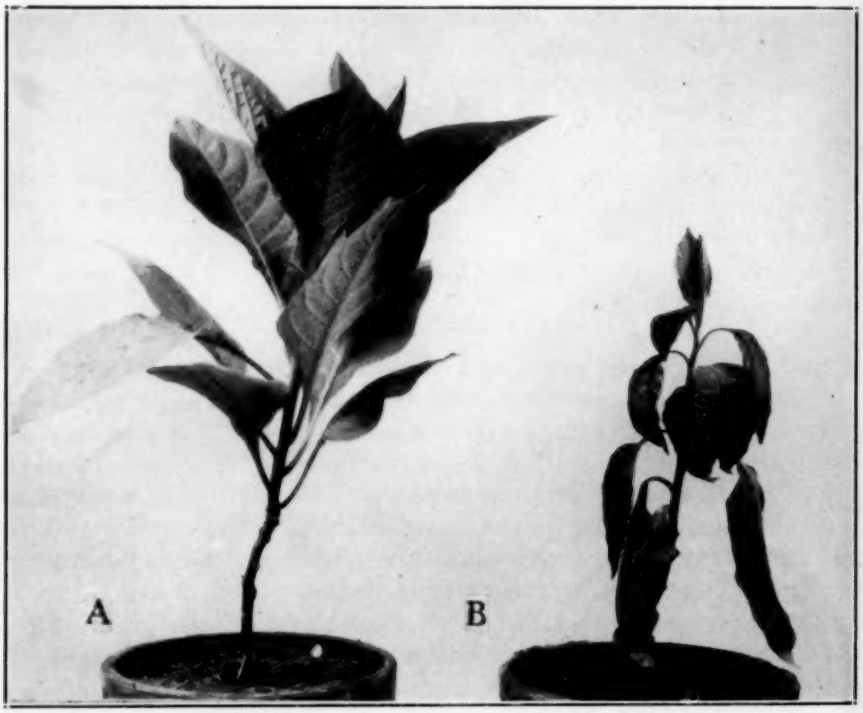

FIG. 3. Phytophthora rot of belladonna: A, noninoculated control; B, symptoms produced by *Phytophthora parasitica* 22 days after inoculation in the greenhouse.

such material. An experiment was devised to determine the ability of *P. parasitica* to cause damping-off of belladonna seedlings. A mixture of one-half sterilized soil and one-half fungus on whole-grain medium was placed in 10 sterile 6-inch pots; this mixture was covered by a thin layer of sterile soil. Five pots contained a mixture of one-half sterilized soil and one-half sterile grain. Fifty belladonna seeds were sown in each of the 15 pots. Four weeks later survival counts were made. In the 10 pots receiving the fungus, the surviving plants numbered: 5, 3, 0, 0, 2, 9, 6, 0, 1, and 4, respectively; in the 5 pots receiving sterile grain (control), the counts were: 37, 41, 26, 39, and 40, respectively.

The pathogenicity of the three *Pythium* spp. was likewise determined. The results showed greatest reduction in stand in the *P. ultimum* series and less reduction in the cases of *P. debaryanum* and *P. irregulare*.

Field observations seem to indicate that one of the principal methods of spread of the disease is through stem and leaf infections of adjoining plants, under conditions of warm air temperatures and high relative humidity. To test this, 49 potted plants were placed in a square group in a moist chamber. Bits of agar containing mycelium and sporangia of *Phytophthora parasitica* were placed in the axils of young shoots on 4 plants comprising the corners of the square border about the center plant. The chamber was atomized continuously with sterile distilled water; light was supplied during the normal daylight hours. Within 3 days infection of the young shoots and attached leaves was observed; the disease began to spread on the fourth and fifth days. Within 10 days the central mass of plants and all but 7 of the marginal plants were infected, the shoots becoming discolored and wilted, the leaves watersoaked and collapsed.

A similar experiment was arranged with 12 plants, in 3 rows of 4 pots each, the 2 center plants being inoculated as described above. After infection had occurred and the disease had begun to spread, atomization was suspended and all plants were sprayed with 2–2–50 bordeaux and a wetting agent, the plants remaining in the moist chamber. The disease was checked, and no further spread occurred over the next 7 days, when the experiment was concluded.

A similar experiment was set up using 14 plants. After the disease began to spread, 2 slightly infected plants were removed to another moist chamber which was wet but not atomized. The other 12 plants were treated exactly as in the previous test. Whereas the disease was checked by the application of bordeaux in the lot of 12 plants, the disease continued to spread in the plants which were not sprayed or atomized. Similar results were obtained by using 2–3–50 burgundy and 1.5–100 yellow cuprous oxide with wetting agent.

CONTROL

No experiments were conducted to determine the origin of infection in field plantings of belladonna, but infection is apparently accomplished in at least two ways: (1) through natural infection of healthy plants by the fungus previously established in the planting area and (2) through the introduction of diseased transplants. The last condition may be controlled through use of seedlings grown in sterile soil.

From field observations it is very evident that belladonna suffers severely from root-rot when grown on heavy soils. The disease also becomes very serious when an overhead irrigation system is employed. Plantings can be suc-

cessfully grown in light soils which are adequately drained and furrow-irrigated rather than sprinkled. The spread of the disease may be substantially reduced through abolishment of the overhead type of irrigation.

Where the disease is established and fungicidal control is necessary, 2–2–50 bordeaux, 2–3–50 burgundy, or 1.5–100 cuprous oxide, with a suitable wetting agent, may be employed to arrest aerial development of the disease.

Damping-off of belladonna may be satisfactorily controlled by seeding in sterile soil, fumigated either with carbon disulfide or with chloropicrin, or steam-pasteurized or autoclaved; sterile pots or flats should also be used. In watering, care should be exercised to avoid splashing water and soil from adjacent unsterilized plant containers. Preliminary investigations in which cuprous oxide, ethyl mercury phosphate, and tetrachloro-parabenzoquinone were used as seed protectants, were rather unsatisfactory, none of these materials effecting adequate control of damping-off.

SUMMARY

Phytophthora rot of belladonna (*Atropa belladonna* L.), occurring in California and affecting roots, crowns, stems, and leaves, is described. This is apparently the first detailed account of a Phytophthora rot of this host in the United States.

The causal organism has been identified as *Phytophthora parasitica* Dastur. The morphology of the fungus is typical of the species. The cardinal temperatures for growth are: minimum, 10° C; optimum 30° to 32.5°; and maximum, 37.5°. The pathogenicity of the fungus to mature and seedling plants has been established.

Control of the disease may be afforded by planting on light, well-drained soils and by the use of the furrow method of irrigation; overhead irrigation should be avoided. Control of the spread of the disease may be accomplished through abolishment of the overhead system of irrigation and the application of bordeaux, burgundy, or cuprous oxide with a suitable wetting agent.

The ability of *Phytophthora parasitica* and of *Pythium debaryanum* Hesse, *P. irregulare* Buis., and *P. ultimum* Trow to cause damping-off of belladonna is likewise described, and the pathogenicity of the fungi is established. Damping-off may be controlled by seeding in sterile soil in sterilized containers. Three materials used as seed-protectant dusts did not effectively control damping-off.

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THE MORPHOLOGICAL NATURE OF THE PHOTOSYNTHETIC ORGANS OF ORCHYLLIUM ENDRESII AS INDICATED BY THEIR VASCULAR STRUCTURE[1]

W. G. McINTYRE AND M. A. CHRYSLER

In spite of the notoriety attained by the "bladders" of the genus *Utricularia*, the morphological nature of the various organs remains unsettled. The aquatic habit appears to have brought about specialization accompanied by reduction. For this reason a mere inspection of the organs and even a comparison of organs in the different genera has led to sharp disagreement. This is illustrated by the selected references which follow.

Schimper (1882) reported his studies on *Utricularia cornuta*, a North American species found along the edges of swamps or on hummocks in moist places. He regarded the underground portions of this plant as branches of the main stem. Certain minute green blade-like organs arising from slender subterranean branches he considered to be of caulome nature.

Schenck (1887) appears to have been the first to have access to a species in which vascular tissues are fairly well developed. He described and presented good figures of the structure of the various organs in *U. montana*, an epiphytic species from the West Indies. He obviously was not impressed by the concentric structure of the "Blattstiel" nor its resemblance to the inflorescence axis, but assumed that the blade-shaped organs are leaves.

Ridley (1888), while describing a specimen of *U. bryophylla*, a small terrestrial species from South Africa, held that the leaf-like organs are of caulome nature because some become narrow toward the tip and continue as bladder-bearing branches.

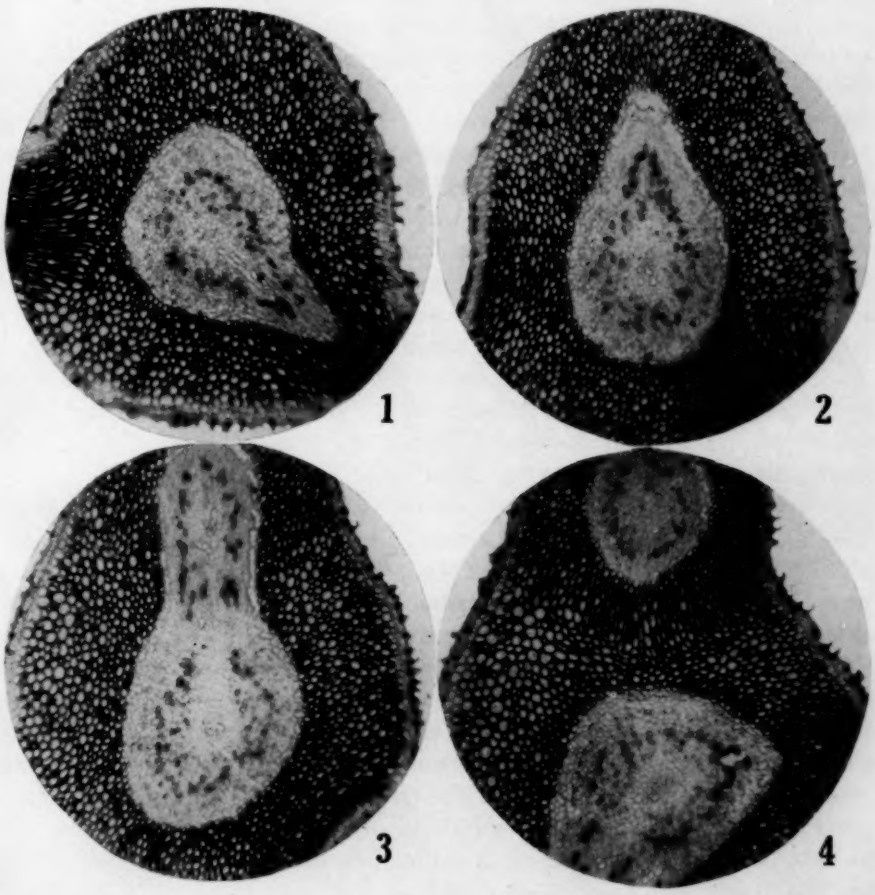
From a study of the South American genus *Genlisea* and several small terrestrial utricularias, Goebel (1898) concluded that all of the lateral organs are modified leaves, that is, all the organs which function as roots and stems are derived from leaves which have become first tubular and then solid branching structures.

In the present study an attempt is made to use the criterion of anatomical structure as exhibited in the Costa Rican species *Orchyllium Endresii* (Rchb. f.) Barnhart, suitably preserved material of which was secured by the second writer in the summer of 1940. Sections were prepared by paraffin and celloidin methods, serial sections being used when desirable. Crystal violet followed by erythrosin was found valuable for differentiating the slightly lignified vessels.

[1] Publication of Bureau of Biological Research, Rutgers University.

In contrast to many members of the family this plant is essentially terrestrial, growing in moss on fallen logs in wet forest, also in peaty matter bearing liverworts and lichens at the surface of crevices in steep banks. As might be expected, the vascular tissues are much better developed than is the case in aquatic members of the family.

The slender inflorescence axis has a height up to 35 cm. and bears from



FIGS. 1–4. Transverse sections through upper part of rhizome, showing mode of exit of vascular supply to the photosynthetic organ (*p*), which in all figures lies toward top of page. Figure 1 is the lowermost section. All ×25. FIG. 1. At lower right hand, early stage in exit of trace to a tuber-bearing branch. At top a slight bulge in xylem indicates beginning of trace supplying *p*. FIG. 2. About 100 μ above level of fig. 1, trace supplying *p* is diverging from stele of rhizome. FIG. 3. About 100 μ above level of fig. 2, trace supplaying *p* is beginning to assume circular outline. FIG. 4. About 100 μ above level of fig. 3, trace supplying *p* shows circular outline. At lower left, the trace of another *p* is leaving stele.

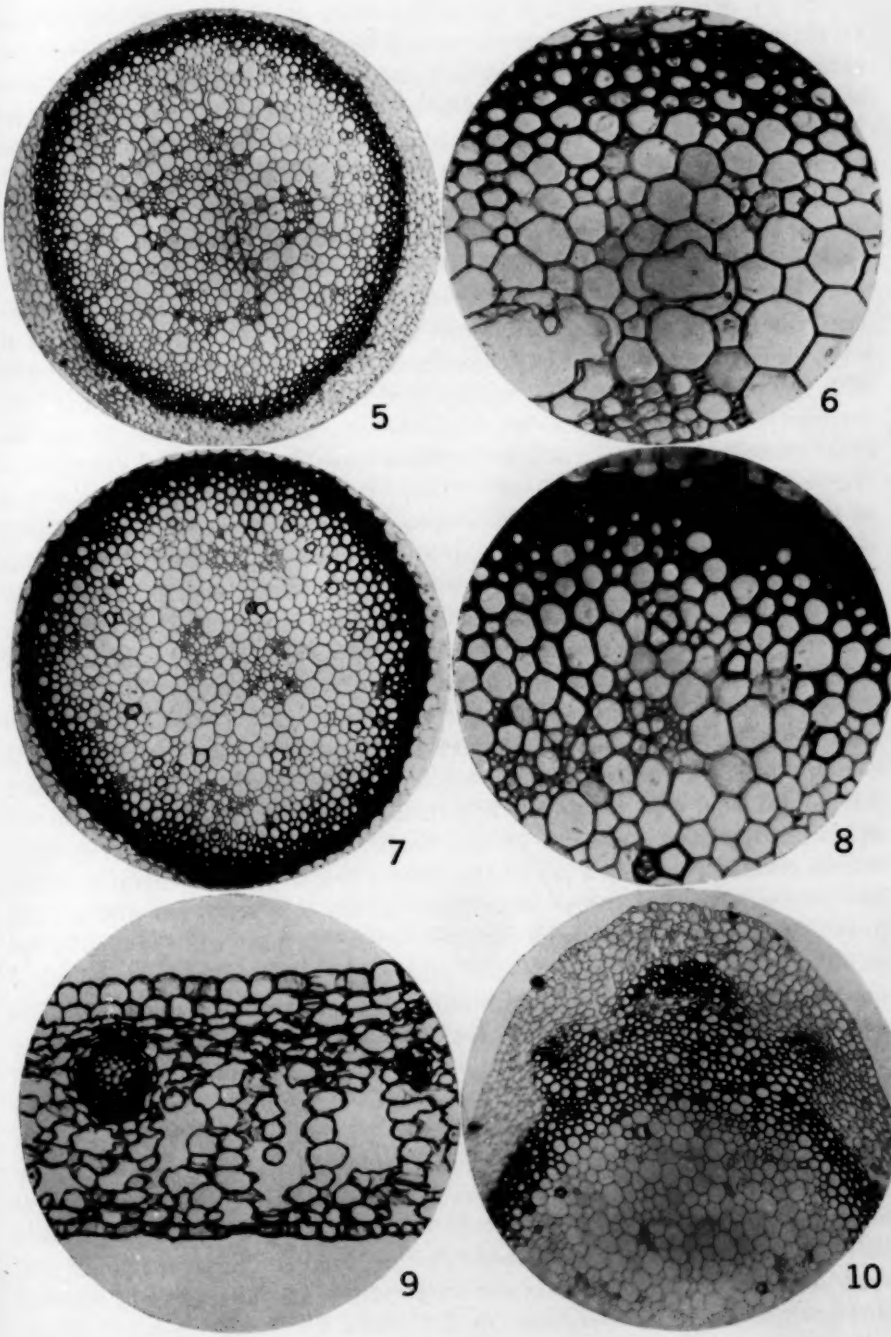
one to five flowers. The large size of the latter (30–40 mm. in width) and their orchid-like appearance as well as the almost epiphytic habit of the plant suggested the name *Orchyllium* to Barnhart (1916) when he segregated the genus from *Utricularia*. Scattered along the axis are several simple lanceolate bracts and at the base of each pedicel are a bract and a pair of bracteoles. The axis forms a vertical extension of the short subterranean stem, which has the appearance of being much condensed. From this stem arise organs of four kinds: (1) the inflorescence axis already mentioned; (2) one or two vertically disposed photosynthetic organs—the so-called leaves; (3) several delicate horizontal or downwardly directed branches bearing minute but perfect "bladders" and functioning as absorbing organs in default of true roots; (4) several stouter branches each of which swells into a translucent tuber 5–8 mm. in diameter and then continues like (3).

The blade of each "leaf" has a length of 40–60 mm. and width of 10–20 mm., is from lanceolate to ovate in shape with the tip acute and the base tapering into the stalk which may have a length of 30–60 mm. There is a pronounced midrib, from which at an acute angle diverge veins which anastomose with one another. The whole organ is inclined to be stiff.

It will now be in place to examine the internal structure of the chief organs. The most conspicuous feature of the rhizome is the wide and thick-walled middle layer of the cortex (figs. 1–4), bounded inwardly and outwardly by narrow layers of thin-walled cells. The epidermis is studded with sac-shaped absorbing hairs. An endodermis is hard to demonstrate, but cells showing a Caspary's band when treated with safranin and fast green form a much interrupted ring bounding the central cylinder. In the stele it will be noticed that the vessels are distributed through an annular zone among thin-walled cells. All of them are narrow (15–30 μ) with spiral or reticulate thickening. Groups of delicate phloem cells (unstained in figures 1–4 but clearly shown in figure 6 representing the inflorescence axis) are scattered through the stele without reference to the xylem. Toward the base of the rhizome the vessels are more or less grouped into bundles with which phloem groups are occasionally associated. The endodermis moreover is readily identified in this region. These observations appear to indicate that the more scattered condition of the vessels and discontinuous nature of the endodermis are due to dilation of the stele.

Explanation of figures 5–10

FIG. 5. Transverse section through inflorescence axis. ×45. FIG. 6. Part of same section. ×175. Six vessels and several phloem groups are shown. FIG. 7. Trans sec. through midrib of photosynthetic organ. ×100. FIG. 8. Part of same section. ×235. Eight vessels, also large and small phloem groups, are shown. FIG. 9. Blade of photosynthetic organ, showing at left a branch of the stele, at lower right a stoma. ×105. FIG. 10. Inflorescence axis at level of exit of the three traces which supply one of the bracts. ×55.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As the rhizome passes into the inflorescence axis (fig. 5) the cortex loses its thick-walled character and consists of four or five layers of parenchyma cells liberally provided with intercellular spaces which are associated with stomata. The stele takes on a new feature, namely, a thick-walled zone about five cells in thickness and lying immediately beneath a clearly marked endodermis. This mechanical layer shades off into the pith. The xylem (fig. 6) continues the annular arrangement characteristic of the rhizome, but the vessels are much less numerous, while a few are to be found in the middle region of the stele; all are thin-walled and poorly lignified but show clearly when stained with crystal violet. The phloem groups are very numerous, some small ones occurring in the mechanical layer and extending quite to its outer edge while several large groups may be present in the middle region of the stele. Thus the vascular tissues of rhizome and inflorescence axis correspond while differing in detail. That the unusual arrangement of the vascular elements is characteristic of *Utricularia* sec. *Orchidoides* (= *Orchyllium* Barnh.) is indicated by Schenck's (1887) figure 5 of the inflorescence axis in *U. montana*. The situation of the vessels among thin-walled cells is a sign of reduction from a more or less continuous xylem cylinder, which reduction is carried so far in the aquatic species that xylem is scarcely discernible. The position of the phloem groups may be interpreted as an extension of the tendency to produce additional phloem groups seen in various members of Solanaceae, Convolvulaceae, and several other sympetalous families.

When we turn to the photosynthetic organs, figure 7 shows the appearance at the level of expansion from stalk to blade. Beneath the epidermis a cortex 4–5 cell layers in thickness is followed by a definite endodermis and a mechanical ring consisting of a few thick-walled layers shading off to the thin-walled cells of the axial ground tissue. This region shows very thin-walled isolated vessels in a peripheral zone, a few in a more central position, and larger or smaller groups of delicate phloem cells scattered through the ground tissue but in this organ rarely invading the mechanical layer, so far as our observations indicate. Several rather large phloem groups are apt to occur in the central region. Longitudinal sections show that the thickenings of the vessels are of the annular, spiral, and reticulate types, all very poorly lignified. Thus point by point the vascular tissues corrsepond in arrangement and structure with those found in the stele of the inflorescence axis. Surely it is just as proper to call the area enclosed by the endodermis a stele as in the two regions of the stem. Small portions of the stele are pinched off to supply the veins of the lamina; the largest of these have a nearly complete mechanical sheath surrounding a very poorly developed central xylem and three or four small peripheral phloem groups; smaller veins show dorsal and ventral mechanical areas, the former frequently being the smaller of the two, with the phloem groups persisting on the flanks. The strands hence resemble

steles rather than collateral bundles. The blade (fig. 9) presents the following layers: (1) an upper epidermis which may have a few glandular hairs of the type occurring on the rhizome; (2) four or five layers of nearly cubical cells, the inner ones containing chloroplasts and reminding one of poorly developed palisade; (3) a spongy layer occupying most of the thickness of the organ; (4) a lower epidermis with stomata of an unspecialized type and glandular hairs in larger numbers than on the upper surface. Obviously the blade would pass for a leaf were it not for the stelar nature of the vascular structures and the similarity of these to the ones found in the stem. It should be remarked that the dorsiventral structure of the blade need not enter into the argument, in view of the fact that the unquestioned flat branches of *Phyllocladus* bear far more stomata on the lower side and show a palisade toward the upper side. These features are to be regarded as strictly ecological.

Schenck's figure 11 (1887) representing the "mid-rib of the leaf" of *U. montana* resembles our figure 7 except that in the former the vessels are somewhat less evenly distributed. Hovelacque (1887) has undertaken to interpret Schenck's figure 6, representing a runner, as showing an arc-formed grouping of the vessels, hence the runner is a phyllome, not a caulome as Schenck held. Realizing that all evidence of dorsiventrality should be considered, and that some of the small vessels may easily be overlooked, we have outlined under high magnification with camera lucida the set of vessels occurring in the section photographed in figure 7. Thirty-four undoubted vessels were found, all but four of them making up an interrupted ring-formed zone, not in any way suggesting an arc. The phloem in our figure looks a trifle suspicious, showing four large groups more or less on an axis running at right angles to the width of the blade, but the illusion is dispelled by a glance at other sections, which show that the phloem groups anastomose so as to present various arrangements. Hovelacque's argument hence appears to have no application to *O. Endresii*, which is probably a more primitive plant than *U. montana* because the former has a better developed primary axis and simpler branches.

Additional light on the morphological status of the photosynthetic organ is afforded by examination of the region where it branches off from the rhizome. Figures 1–4 represent sections selected from a series taken through the stem. Reference is made to the legend, which sufficiently indicates that the vascular system of the so-called leaf arises as a concentric group, not a collateral one; that is, we are here dealing with a flattened branch, not a leaf. It is instructive to compare these sections with those cut from an inflorescence axis at the level of origin of one of the bracts. In spite of its small size the bract is supplied by three vascular bundles, arising separately from the stele of the axis (fig. 10), the median bundle being larger than the laterals. It

will be recalled that this is the typical mode of origin of the vascular supply of a leaf. The contrast between figures 10 and 3 is sufficiently striking. In sections through a bract the median bundle is represented by 4–6 vessels arranged in a broken row parallel with the surface of the bract; applied abaxially to these several minute groups of phloem; finally a conspicuous island of mechanical fibres—essentially a collateral bundle.

Plainly *Orchyllium* has not entirely lost the power of producing leaves, and these are unmistakable when they do occur. It would naturally be gratifying to find a leaf or bract subtending a photosynthetic organ, comparable with the bract occurring at the base of each cladophyll in *Ruscus*, but nothing of the kind appears to be present. This seems to be one of the features of reduction in this very specialized subterranean organ. It will be recalled that the bract which usually subtends each flower of a raceme is typically absent in Cruciferae.

Petioles showing a stele-like bundle are of course known in different groups of plants; for example, several species of the fern genus *Gleichenia* show a concentric arrangement of xylem and phloem and even a pith area in certain regions of the leaf axis; but this represents a pseudostele, formed by fusion of the edges of a C-shaped leaf trace, as was pointed out by Jeffrey and others. Likewise the concentric structure seen in the petiolar bundle of some species of *Primula* has been shown by Gwynne-Vaughan (1897) to be the result of the same process as occurs in *Gleichenia*. In *Orchyllium*, however, the concentric trace supplying the photosynthetic organ arises in a quite different manner, as we have shown.

In view of the evidence derived from internal structure, the inference appears inescapable that in *Orchyllium* the photosynthetic organs are not leaves but flattened stems of limited growth, hence the name cladode is applicable. Naturally the early students of the bladderworts interpreted the organs by comparing the external form in various species and genera. Even Schenck, who made a careful study of *U. montana*, apparently failed to perceive the implication of the vascular structures exhibited in this close relative of *O. Endresii*, for without comment he called the green organs "leaves." But this was in 1887. Meanwhile it has come to be realized that the vascular parts of a plant are less liable to modification by reason of changes in the environment than is the external form. Hence the vascular anatomy furnishes one of the most reliable criteria for establishing morphological concepts and for determining relationships. Goebel was an earnest student of the group, but even in his later contributions paid scant attention to vascular structures. He reached the somewhat disconcerting conclusion that in *Utricularia* and its allies: "kurtz es ist das gewöhnliche Schema der Organbildung hier ganz über den Haufen geworfen." (Goebel 1898, p. 446). His trans-

lators have rendered the last phrase as "jumbled," which probably expresses the meaning rather mildly.

The anatomical evidence furnished by such terrestrial species as *O. Endresii* and *U. montana* is so consistent that it becomes probable that the small green blade-like organs arising from the creeping stem of *U. cornuta* are also of caulome nature, as was suggested by Schimper (1882). Barnhart's study of the family led him on the basis of external features such as bracts to place his new genus *Orchyllium* next to Rafinesque's genus *Stomoisia*, which includes the former *U. cornuta* and other species. These near-aquatics naturally have practically no vascular tissues, but have in all probability been derived from terrestrial plants, so that the systematic position of *Stomoisia* and other segregates may be significant.

We are not prepared however to extend the cladode theory to all members of the family. The vascular structures in the different genera show considerable differences. Thus Van Tieghem (1869) reported that in *U. vulgaris* the stele has a narrow central vessel surrounded by elongated cells containing a granular liquid. This is a reduced condition of the xylem which is shown by other aquatics, e.g., *Elodea*. Dangeard and Barbé (1887) observed in *Pinguicula* the condition which they called polystely and compared with the similar condition in *Primula Auricula*. Merl (1915) furnished an account of the anatomy of several species of *Genlisea*, finding in all a sclerenchymatous ring surrounding a circular series of phloem groups, with vessels distributed through the pith. It will be noticed that none of these plants has an arrangement of vascular tissues like that described by Schenck (1887) and the present writers. In view of this diversity in the vascular tissues, it would be unwarranted to claim that cladodes occur throughout the family. *Pinguicula*, *Genlisea*, and *Utricularia* are so different in various respects that the family must have had a long history which is at present unknown. Goebel may well be correct in regarding all the organs of *Genlisea* as modified leaves, but the observations presented in this paper strongly support the earlier view of Schimper and others that the flattened organs in *Utricularia, sensu lato*, are of the nature of branches.

SUMMARY

The problem of the morphological nature of the photosynthetic organs in *Utricularia* is approached from the point of view of vascular structure in the terrestrial tropical *Orchyllium Endresii*. In this species the vascular tissues are fairly well developed, and so-called leaves are conspicuous organs.

The stele of the underground stem presents a ring-formed group of vessels interspersed in much parenchyma, and numerous small groups of phloem cells scattered through the stele. The inflorescence axis has a similar structure, with vessels more scattered. The stalk of the "leaf" is constructed

almost exactly like the preceding organ, and its vascular supply arises from the stele of the stem as a concentric rather than collateral organ.

The only organs with leaf structure are the bracts on the inflorescence axis. The vascular supply of a bract consists of a median and two smaller lateral bundles arising separately from the stele of the inflorescence axis.

These observations indicate that the so-called leaf of *Orchyllium* is to be regarded as a specialized branch or cladode. It is suggested that cladodes may be present in aquatic members of the family in which vascular tissues are reduced to the vanishing point.

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POLYPLOIDY IN SEDUM PULCHELLUM—II. STOMATAL SIZE AND FREQUENCY[1]

HARRIET E. SMITH

Within recent years it has been found that in many groups of plants polyploids can be distinguished from diploids by comparing the size and frequency of stomata. An increase in chromosome number is accompanied by an increase in stomatal size and a decrease in stomatal frequency in *Zea* (Randolph 1932, 1935), *Tradescantia* (Sax & Sax 1937), *Coffea* (Franco 1939), and other genera. It has been suggested that such a relationship between stomata and chromosome number would aid in detecting polyploid races in herbarium material, and stomatal size and frequency have actually been so used as criteria for polyploidy (Babcock & Stebbins 1938; Stebbins 1939; Sax & Sax 1937). This also offers a ready clue toward determining polyploid races of living plants.

To ascertain the size and frequency of stomata in *Sedum pulchellum*, studies were made on the diploid ($2n = 22$), tetraploid ($2n = 44$), and hexaploid ($2n = 66$) races. Counts were made on the diploid for 19 plants from 16 locations, on the tetraploid for 19 plants from 12 locations, and on the hexaploid for 12 plants from 3 locations.[2] The chromosome counts were made by J. T. Baldwin, Jr., from aceto-carmine smears of roots and leaves, and some from Nawaschin-fixed, crystal-violet-stained sections of roots.

Since environmental conditions and position of leaf on the plant have been found to affect the size and distribution of stomata in some species (Franco 1939; Hirano 1931), the plants studied were grown under uniform conditions and counts were made only from basal juvenile leaves of plants at a uniform stage of development. Although preliminary observations indicated that stomatal size and frequency do not vary appreciably in the same leaf in *Sedum pulchellum*, an attempt was made always to take the count from the middle portion of the lower epidermis of the leaf.

Lloyd's method (Lloyd 1908) for measuring stomata was used: the lower epidermis was stripped from the leaf and fixed at once in absolute alcohol (Lloyd found no measurable shrinkage of stomatal size under this treatment). Measurements of five open stomata on each leaf were made with an eyepiece micrometer, a Spencer microscope with a 10× ocular and 44× objective being used; stomatal counts were made with a 10× ocular and

[1] Papers from the Department of Botany of the University of Michigan, No. 816.

[2] Collections were made by: J. T. Baldwin, Jr., Jean M. Campbell, L. M. Dickerson, R. M. Harper, A. M. Harvill, Milton Hopkins, D. W. Moore, H. T. Shacklette, J. A. Steyermark, Mary E. Wharton.

10 × objective; the total number of stomata per microscopic field was determined and the statistical comparison of races was based on the number of stomata per field. The numbers were converted later to number of stomata per square millimeter.

Individual plants in each race vary so greatly morphologically that it would be hazardous to judge the degree of polyploidy by the general appearance of a single plant; however, when large numbers of plants of different races are studied, racial differences can be discovered. In the diploid, the juvenile leaves are small and densely crowded, giving the plant a compact appearance. In the tetraploid, leaves are slightly darker in color, larger, and not so densely crowded. The tetraploids appear to be healthiest and most vigorous. Hexaploid leaves are broadest, and in length are intermediate between those of the diploid and the tetraploid (fig. 1). The hexaploid has

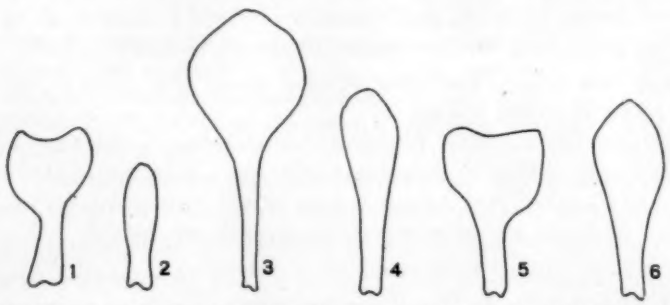

FIG. 1. Primary and secondary juvenile leaves of *Sedum pulchellum*. 1. Primary leaf of diploid, $2n = 22$. 2. Secondary leaf of diploid. 3. Primary leaf of tetraploid, $2n = 44$. 4. Secondary leaf of tetraploid. 5. Primary leaf of hexaploid, $2n = 66$. 6. Secondary leaf of hexaploid. All × 2.

fewer but longer stems than the tetraploid, giving the hexaploid a more diffuse appearance. Measurements of mature leaves are being analysed statistically and will be published later. Diploids mature and flower earlier than the other two races. The three races occupy different geographical regions (Baldwin 1942).

Stomatal size was found to vary directly with chromosome number, and stomatal frequency inversely with chromosome number (table 1). The differences in the means of the different races all give very high values of *t*,

TABLE 1. *Stomatal Size and Frequency in Sedum pulchellum*

Chromosome number	Number of plants	Mean stomatal size in μ	Mean number of stomata per field	Mean number of stomata per sq. mm.
$2n = 22$	19	269 ± 3	83.3 ± 2.125	697
$2n = 44$	19	457 ± 8	53.6 ± 1.005	449
$2n = 66$	12	575 ± 6	42.75 ± 1.5	358

the smallest being $t = 6$; therefore these differences are statistically highly significant.

It must be emphasized that environmental conditions and other factors as well as chromosome number can strongly influence the frequency of stomata. In an attempt to learn how polyploidy exerts effect, therefore, it should be worth while to study the influence of environment upon the size and distribution of stomata. Yapp (1912), Salisbury (1927), and Maximov (1929) have found stomatal frequency to be correlated negatively with water supply: sun leaves have more stomata per unit area than shade leaves; plants grown under dry conditions have more stomata than those under humid conditions; upper leaves of many herbs and shrubs have more stomata than lower leaves, the upper leaves being farther from the source of water supply. Yapp and Salisbury consider high stomatal frequency to be a xeromorphic character. Maximov and Salisbury have found that in plants having more stomata on the upper leaves than on the lower ones, the upper leaves have a greater osmotic pressure than the lower ones. Thus high stomatal frequency appears to be correlated with high osmotic pressure. Yapp and Maximov in discussing the cause of high stomatal frequency in the upper leaves of a plant advance the theory that high stomatal frequency is actually caused by high osmotic pressure in the leaf while the leaf is developing and expanding. Although in this study on *Sedum* no attempt has been made as yet to determine osmotic pressures of the different chromosome races, Becker (1931), working with mosses, found osmotic pressure to be inversely proportional to chromosome number. If this should be found to be a general characteristic of polyploidy, then the high stomatal frequencies of the diploids and low frequencies of the hexaploids would be correlated with differences in osmotic pressure and would, accordingly, agree with Yapp's theory.

The ecological significance of stomatal size and frequency is somewhat uncertain. Salisbury (1927), in his study on the ecological significance of stomatal frequency, concludes that since the correlation between number of stomata and humidity is negative, stomatal frequency has no adaptational significance in relation to transpiration or assimilation. Yapp (1912), on purely theoretical grounds, concludes that the transpiration rate through the smaller but more numerous stomata of xeromorphic leaves should not be much greater than that through the larger but fewer stomata of less xeromorphic leaves, but Smith (1941) has found a significant positive correlation between stomatal frequency and transpiration in *Phaseolus vulgaris*.

SUMMARY

Stomatal size and frequency in juvenile leaves of three races of *Sedum pulchellum* were determined: stomatal frequency varies inversely with chromosome number; stomatal size varies directly with chromosome number.

When grown under constant environmental conditions, the three races differ morphologically, but there is also great variation within each race.

A possible relationship between chromosome number, osmotic pressure, and stomatal size and frequency is suggested.

The ecological significance of stomatal size and frequency is uncertain.

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THE NORTH AMERICAN SPECIES OF ERIGERON CENTERING ABOUT E. SPECIOSUS (LINDL.) DC. AND E. GLABELLUS NUTT.

ARTHUR CRONQUIST

In the course of preparing a revision of the North American species of *Erigeron*, I think it advisable to place the following treatment of some western species on record, in order that certain names and combinations may be made available for use. Citation of specimens, and discussions of phylogeny and evolutionary trends, are reserved for inclusion in a later more extensive work.

This study is intended to include the biennial and perennial North American species of *Erigeron* that have double pappus and erect stems with broad cauline leaves, exclusive of *E. philadelphicus* L. and its immediate relatives. Roughly, it includes the sections *Macranthi*, *Glabelli*, and *Asperi* of Dr. Rydberg's treatments. These forms constitute an entirely natural group.

As in many genera of the *Compositae*, complete morphologic discontinuity between species does not always exist. Intermediates can be found between forms that by any reasonable taxonomic system must be recognized as valid species. Those units which are comparatively distinct from other units, and whose subunits, if any, all share some common character or characters not found in closely related units, have been recognized as species. Geographic distribution of each of the groups recognized as a species is fairly continuous.

Following immediately on the question of specific criteria is the problem of intraspecific units. I wish to place on record here my concept of these.

Subspecies: An intraspecific unit, more or less genetically continuous through time because of a tendency for its individuals to breed largely among themselves, which occupies a largely distinct range of its own, and intergrades with other units where their ranges meet; or, a group of varieties that are more closely related to each other than to other varieties of the species.

Variety: An intraspecific unit, more or less genetically continuous through time because of a tendency for its individuals to breed largely among themselves, which shares a large part of its range with similar units, or which occurs anywhere within the range of a given species or subspecies.

Form: A minor intraspecific unit which occurs sporadically through part or all of the range of a species or major intraspecific unit, does not occupy any sizeable area to the exclusion of other individuals of the species, and

whose individuals show no obvious tendency, other than that induced solely by proximity, to breed largely among themselves.

In any monographic work, the nomenclaturally typical unit of a species should receive the conventional varietal or subspecific epithet if there are any major units within the species. It is not desirable, however, to grant the typical unit an epithet as a *forma*, unless, as is not usually done, all of the formae of that species are treated and named.

It is my conception that any real subspecies or variety will probably have some habitat preferences or peculiarities of its own developed to a greater or lesser degree, so that it is not necessary to grant subspecific status to ecotypes which are not geographically segregated.

The criteria used in this treatment are mostly external and superficial, such as the width of the phyllaries, size and distribution of the leaves, and pubescence. Width of the phyllaries, hitherto apparently almost totally disregarded, seems to be of considerable importance. Each of the species varies about its own mean, with the extremes commonly overlapping the extremes of certain other species. The width of the phyllaries is particularly helpful in distinguishing doubtful forms of *E. superbus* from *E. speciosus*, and *E. formosissimus* from *E. subtrinervis*. Associated with phyllary width is the degree of looseness of the tips. *E. superbus*, *E. formosissimus*, and *E. glabellus* are notable for the comparatively close tips of the phyllaries in mature heads, while *E. speciosus* and *E. subtrinervis* are notable for the very loose tips of the phyllaries.

Distribution and relative size of the leaves are very helpful. With the exception of *E. superbus*, the group may be divided into those forms in which the basal leaves are largest and the upper ones progressively and conspicuously reduced, and those in which the middle leaves are as large as or somewhat larger than the basal ones, with the upper ones only gradually reduced.

Type and distribution of pubescence are generally helpful, each unit here recognized having its own characteristic vesture. Number and width of ligules are occasionally helpful, as are height of the plant and persistence or deciduousness of the basal leaves. Size and number of heads, and shape of the inflorescence have only very limited usefulness, being too variable in most of the species to be of much help. Length and color of the ligules, and character of the short outer pappus seem to be wholly unreliable in this group of species. More technical characters of the achenes and disc corollas are in general too uniform to be of much value in the group.

About 2500 sheets, from 15 herbaria, have been assembled for this study. I wish to thank the curators for their kindness in loaning specimens. Grateful acknowledgement of assistance is made to Dr. Ray J. Davis, who has spared no effort to assemble the necessary materials and has given continued

advice and encouragement, to Dr. Bassett Maguire, who has been most generous in providing access to necessary literature, and to my wife, Mabel Allred Cronquist, who has assisted and encouraged the study in various ways.

KEY TO THE SPECIES

1. Stem leaves glabrous or glandular, not even ciliate on the margins, comparatively few and little if at all longer than the internodes ..... 1. *E. superbus*
1. Stem leaves either obviously pubescent or at least ciliate on the margins, sometimes also glandular, often numerous and longer than the internodes.
2. Plant rather equably leafy, the upper stem leaves gradually rather than conspicuously reduced, the middle stem leaves commonly larger than the lowermost ones.
3. Upper and middle stem leaves glabrous or nearly so except for the ciliate margins; stem glabrous below the inflorescence or bearing a few scattered hairs ..... 2. *E. speciosus*
3. Upper and middle stem leaves obviously hairy or glandular or both, or the stem conspicuously pubescent with long spreading hairs.
4. Leaves glandular or glandular-scabrous, sometimes also sparsely long-hairy.
5. Leaves without long eglandular hairs except for the ciliate margins and occasional long hairs along the midribs; stem pubescent above with stiff spreading hairs; plants of Arizona and New Mexico ..... 3. *E. platyphyllus*
5. Leaves and stem sparsely pubescent with long, soft, flexuous hairs; plants of southwestern Wyoming to central Utah ..... 4. *E. wintahensis*
4. Leaves hairy, not glandular or the uppermost ones but slightly glandular ..... 5. *E. subtrinervis*
2. Plant rather inequably leafy, the upper leaves conspicuously reduced, the middle ones commonly smaller than the lowermost ones.
3. Stem and involucre glandular or viscid, sometimes also hairy. 6. *E. formosissimus*
3. Stem and involucre more or less hairy, not at all glandular or viscid ..... 7. *E. glabellus*

TREATMENT OF THE SPECIES

1. ERIGERON SUPERBUS Greene ex Rydb. Colo. Exp. Sta. Bull. 100: 351, 364. 1906. *E. apiculatus* Greene, Leafl. **2**: 217. 1912. *E. eldensis* Greene, Leafl. **2**: 196. 1912. *E. macranthus* subsp. *mirus* A. Nels. Proc. Biol. Soc. Wash. **17**: 178. 1904.

Perennial herbs arising from simple or slightly branched caudices, commonly bearing tufts of radical leaves at the ends of short rhizomes; stems 1 or several, 1.5–6 dm. high, glabrous below, glandular in the inflorescence; leaves more or less triple-nerved, few, commonly shorter than or barely exceeding the internodes, obtuse or acute, apiculate, entire or some, especially the lower, denticulate or crenulate, not ciliate on the margins, or the lowermost but slightly so toward the bases of the petioles; basal and lowermost cauline leaves glabrous, persistent, oblanceolate to oval, rather abruptly narrowed to winged petioles, the blade and petiole 3–15 cm. long and 10–33 mm. wide;[1] middle cauline leaves smaller than or equalling those below, lanceolate to oblong or ovate, glandular; heads mostly 1–7, rarely as many

[1] Here and elsewhere figures for width of leaf refer to maximum width of blade.

as 16, commonly cymose and borne on nearly naked peduncles, the discs 11–19 mm. wide and 6–10 mm. high; phyllaries in one or two equal series, glandular, occasionally with a few long hairs, the outer ones broad, mostly 0.8–1.3 mm. wide, acuminate, the tips appressed or a little loose; ligules comparatively few, mostly 40–80, 1–2 mm. wide and 12–20 mm. long, blue or rose-purple, rarely white; pappus double, the outer setulose and sometimes very scanty. Mountains; southern Wyoming, Colorado, Utah, New Mexico, and Arizona. Not common.

Erigeron superbus has sometimes been regarded as conspecific with *E. eximius* Greene, which was published several years before *E. superbus*. Through the kindness of Dr. Theodor Just, the type of *E. eximius* in the Greene herbarium at Notre Dame has been carefully checked and photographed. It is *E. formosissimus*, variety *viscidus*, with which *E. superbus* intergrades to some extent.

2. ERIGERON SPECIOSUS (Lindl.) DC. Prodr. **5**: 284. 1836.

Perennial herbs with more or less branched woody caudices; stem 1.5–8 dm. high, glabrous, or sometimes slightly hairy or glandular in the inflorescence, usually with a few hairs just under each head; leaves commonly but not always triple-nerved, entire but with ciliate margins, the cilia sometimes very few or present only along part of the margin, glabrous or sometimes with a few hairs along the main veins, the basal and lowermost cauline ones oblanceolate to broadly spatulate, narrowed to winged petioles, the blade and petiole mostly 5–15 cm. long and 4–20 mm. wide, usually deciduous or withered by flowering time; middle cauline leaves as large as the lower, or commonly larger, narrowly lanceolate or oblong to broadly ovate or oval, acute or sometimes obtuse, apiculate, sessile, 3–11 cm. long and 5–28 mm. wide; upper leaves usually not markedly reduced, narrowly lanceolate to broadly ovate, occasionally minutely glandular; heads 1–13, cymose or cymose-paniculate, the discs 6–13 mm. high and 11–22 mm. broad; phyllaries in about two equal series, glandular and sometimes with a few long hairs, the outer ones mostly 0.4–0.8 mm. wide, acuminate or attenuate, the tips loose; ligules numerous, about 75–150, about 1 mm. wide, 9–18 mm. long, blue, rarely white; pappus double, the outer commonly setulose. Mountains and woodlands; southern British Columbia and Alberta to northern Oregon, eastward and southward to Montana, western South Dakota, New Mexico, and Arizona; an isolated station in the Sierra San Pedro Martir, Baja California.

1. Uppermost leaves lanceolate; phyllaries commonly with a few hairs ..... a. var. *typicus*
1. Uppermost leaves ovate; phyllaries without hairs ..... b. var. *macranthus*

2a. **Erigeron speciosus** (Lindl.) DC. var. **typicus,** Cronquist var. nov. *Stenactis speciosa* Lindl. Bot. Reg. **17**: *pl. 1577*. 1833. *E. speciosus* DC. Prodr. **5**: 284, as to type. 1836. *E. salicinus* Rydb. Bull. Torrey Club **32**: 125. 1905.

Stem sometimes slightly hairy above; uppermost leaves lanceolate, often strongly ciliate all around, sometimes with a few hairs on the surface; phyl-

laries commonly with a few hairs. Range of the species, but most common in British Columbia, Washington, Oregon, and northern Idaho.

2b. **Erigeron speciosus** (Lindl.) DC. var. **macranthus** (Nutt.) Cronquist, comb. nov. *E. macranthus* Nutt. Trans. Am. Phil. Soc. II. **7**: 310. 1841. *E. Vreelandii* Rydb. Bull. Torrey Club **32**: 125. 1905. (See note under *E. platyphyllus* Greene.) *E. eucephaloides* Greene, Leafl. **2**: 216. 1912. *E. leiophyllus* Greene, Leafl. **2**: 218. 1912.

Stem commonly glabrous except directly under the heads; uppermost leaves ovate, rarely strongly ciliate all around, not at all hairy on the surfaces; phyllaries without hairs. Range of the species, but most common from Idaho and Montana southward.

E. speciosus and *E. macranthus* have long been accepted as distinct species, the former supposedly found in the Pacific Northwest, the latter in the Rocky Mountains. Rydberg, and later Blake, recorded *E. speciosus* from the Rocky Mountains, and shortly thereafter Blake named specimens from Washington *E. macranthus*. Examination of the two forms indicates that there is some degree of range correlation, but that either may be expected occasionally in any part of the range. The distinction between the two forms is indeed so tenuous that a good case could be made out for complete reduction of *E. macranthus* to synonomy. Its status as a variety is very weak.

3. Erigeron platyphyllus Greene, Leafl. **1**: 145. 1905. *E. foliosissimus* Greene, Leafl. **2**: 194. 1912. *E. patens* Greene, Leafl. **2**: 194. 1912. *E. rudis* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 184. 1913. *E. semirasus* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 185. 1913.

Perennial herbs with branched woody caudices; stems coarse and stout, 3–8 dm. high or more, only rarely less than 5 dm. high, pubescent at least above with long stiffly spreading hairs, often glandular as well; leaves crowded, more or less triple-nerved, entire but with strongly ciliate margins, at least the middle and upper ones rather densely glandular or more commonly glandular-scabrous, rarely with a few long hairs along the midribs, the basal and lowermost cauline ones oblanceolate to spatulate, narrowed to winged petioles, the blade and petiole mostly 4–15 cm. long and 7–25 mm. wide, often deciduous or withered by flowering time; middle cauline leaves as large as those below, lanceolate to oblong or ovate, sessile, 4–11 cm. long and 10–25 mm. wide, upper leaves not markedly reduced, narrowly lanceolate to narrowly ovate; heads 1–22 in a usually short and broad leafy cyme or cymose panicle, the disks 10–15 (rarely 18) mm. wide and 5–9 mm. high; phyllaries in about two equal series, glandular and sometimes with a few long hairs, the outer ones mostly 0.5–0.9 mm. wide, noticeably broadest near the bases, acuminate, the tips a little loose; ligules numerous, mostly 75–150, about 1 mm. wide and 9–17 mm. long, blue or rarely rose; pappus double. Mountains and woodlands; New Mexico and Arizona.

This species has long passed as a form of *E. macranthus*. The glandular-scabrous leaves and conspicuous spreading hairs on the stem adequately set

it off from that form, although intermediates may be found. Dr. S. F. Blake has recently used the name *E. patens* Greene for this species. Unfortunately, *E. platyphyllus* Greene antedates *E. patens*, and hence must be used, although the cited type is not a very representative form of the species.

E. Vreelandii Rydb., the type of which comes from southern Colorado, just outside the known range of *E. platyphyllus*, was published several months before *E. platyphyllus*. An isotype at hand has distinctly glandular middle and upper leaves, as in *E. platyphyllus*, but lacks the characteristic spreading hairs on the stem. Probably it represents an extreme form of *E. speciosus* var. *macranthus*, the uppermost leaves of which are sometimes very finely glandular. Possibly it may be a hybrid, but I have seen no specimens of *E. platyphyllus* from the area in which it was collected.

4. **Erigeron uintahensis** Cronquist, sp. nov.

Perennial herbs with more or less branched woody caudices; stem 2–5 dm. high, glandular at least above, rather sparsely pubescent throughout with spreading several-celled hairs sometimes as much as 2 mm. long; leaves entire, but with ciliate margins at least toward their bases, the basal and lowermost cauline ones villous-hirsute, sometimes also glandular, oblanceolate, tapering gradually to winged petioles or petioliform bases, the blade and petiole mostly 4–10 cm. long and 6–18 mm. wide, often deciduous by flowering time; middle cauline leaves as large as those below, or larger, oblong or lanceolate to ovate or oval, sessile and somewhat clasping, 3–10 cm. long and 8–20 mm. wide, more or less glandular and sparsely long-hairy; upper leaves not markedly reduced, ovate or lanceolate, glandular and commonly with a few villous hairs; heads 1–5, cymose, the disks 6–9 mm. high and 12–18 mm. broad in pressed specimens; phyllaries in about two equal series, densely glandular and bearing a few villous hairs, the outer ones mostly 0.5–0.9 mm. wide, acuminate or attenuate; ligules numerous, about 75–125, about 1 mm. wide, 9–15 mm. long, blue or rose-purple; pappus double. Uintah Mountains and adjacent area, extending down the Wasatch and adjacent chains to Marysvale, occasional in southern Wyoming.

Herba perennis 2–5 dm. alta parce villosa pilis flexis dispansis certe supra glandulosa aequabiliter foliosa foliis integris, capitulis 1–5 discis 6–9 mm. altis 12–18 mm. latis, bracteis 2-seriatis valde glandulosis et parce villosis, ligulis 75–125, 1 mm. latis 9–15 mm. longis caeruleis, pappo duplico, achaeniis 2-nervosis.

TYPE: *Payson 4894*. Mill Creek, foothills of the Uintah Mountains, sandy river bottom, 8200 feet, July 4, 1926, Summit County, Utah; in the Rocky Mountain herbarium. Isotypes in the herbaria of the University of California, the Missouri Botanical Garden, the United States National Herbarium, and Washington State College.

COTYPE: *Goodman & Hitchcock 1548*. Bear River Valley, dry sagebrush flats, 7900 feet, July 9–13, 1930, Summit County, Utah; in the herbaria of the University of California, the University of Minnesota, the Missouri Botanical Garden, and the Academy of Natural Sciences of Philadelphia.

This endemic has until now passed unrecognized, having been identified by various individuals as *E. speciosus*, *E. macranthus*, *E. viscidus*, and *E.*

subtrinervis, often with a question mark. It is apparently not uncommon in the lower part of the Uintah Mountains, from which about a dozen collections are known. Two collections are known from adjacent Wyoming, and a few from the Wasatch Mountains and their southern extensions. In the Uintahs it is surprisingly constant in appearance, but some specimens from the Wasatch are dubious and perhaps intermediate with *E. speciosus* or *E. subtrinervis*. Its closest relative seems to be *E. platyphyllus*, and the trail of atypical specimens down the Wasatch may represent remnants of an earlier link between the two forms.

5. ERIGERON SUBTRINERVIS Rydb. Mem. Torrey Club **5**: 238. 1894.

Perennial herbs with more or less branched woody caudices; stem 1.5–9 dm. high, pubescent throughout with spreading hairs; leaves more or less triple-nerved, entire but with ciliate margins, densely pubescent along the veins or more or less pubescent throughout, the basal and lowermost cauline ones mostly oblanceolate, narrowed to winged petioles, the blade and petiole mostly 4–13 cm. long and 5–23 mm. wide, often deciduous by flowering time; middle cauline leaves as large as those below, narrowly lanceolate or oblong to broadly ovate, sessile, 3–8 cm. long and 6–27 mm. wide; upper leaves not markedly reduced, narrowly lanceolate to ovate, rarely a little glandular; heads 1–21, cymose or cymose-paniculate, the disks 6–9 mm. high and 13–20 mm. broad; phyllaries in about two equal series, glandular and more or less hirsute or villous, the outer ones mostly 0.4–0.7 mm. wide, acuminate or attenuate, the tips loose; ligules numerous, about 100–150, about 1 mm. wide, 7–18 mm. long, blue or rose-purple; pappus double, the outer commonly setulose. Mountains and woodlands; Washington and Idaho, east to western South Dakota and Nebraska, and south to Utah and New Mexico.

1. Pubescence of the stem and leaves commonly rather dense and uniformly distributed, not obviously denser along the veins; longer hairs of the stem mostly about 1 mm. long or less ..... a. subsp. *typicus*
1. Pubescence of the stem and leaves commonly rather sparse and long, on the leaves often confined chiefly to the margins and larger veins; longer hairs on the stem mostly 1½ mm. long or more ..... b. subsp. *conspicuus*

5a. ERIGERON SUBTRINERVIS Rydb. subsp. **typicus** Cronquist, subsp. nov. *E. glabellus* Nutt. var. *mollis* Gray, Proc. Phil. Acad. **1863**: 64. 1864. *E. subtrinervis* Rydb. Mem. Torrey Club **5**: 238, as to type. 1894. *E. incanescens* Rydb. Bull. Torrey Club **28**: 23, 1901. *E. Bakeri* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 185. 1913.

Pubescence commonly uniformly distributed and rather dense, if sparse, that on the leaves not confined to the margins and larger veins; longer hairs of the stem mostly 1 mm. long or less, or if obviously longer, then the leaves very densely pubescent. Wyoming, Utah, and New Mexico, east to western Nebraska and South Dakota.

5b. ERIGERON SUBTRINERVIS Rydb. subsp. **conspicuus** (Rydb.) Cronquist, comb. nov. *E. conspicuus* Rydb. Mem. N. Y. Bot. Gard. **1**: 400. 1900. *E. villosulus* Greene, Leafl. **2**: 215. 1912.

Pubescence sparse and long, that on the leaves denser on the margins and main veins, and sometimes confined chiefly thereto; longer hairs on the stem mostly 1½ mm. long or more. Washington, Idaho, Montana, and northwestern Wyoming.

Herbarium records, and my own limited field experience with it, indicate that this species frequents somewhat drier habitats than does its close relative, *E. speciosus.*

6. ERIGERON FORMOSISSIMUS Greene, Bull. Torrey Club **25**: 121. 19 Mr 1898.

Perennial herbs with simple or somewhat branched caudices and fibrous root systems; stems 1–4 (rarely 5.5) dm. high, usually curved or decumbent at the base, more or less glandular at least above, with or without eglandular hairs; hirsute, glandular, or glabrous below; basal and lowermost cauline leaves commonly glabrate or with long scattered hairs, sometimes densely pubescent, oblanceolate or spatulate to oval, entire, commonly rounded or obtuse at the tips, sometimes acute, abruptly narrowed to winged petioles or petioliform bases, the blade and petiole if present mostly 2.5–15 cm. long and 4–15 mm. wide; middle stem leaves lanceolate or oblong, sometimes ovate, commonly somewhat smaller than the lower ones, mostly 2–6 cm. long and 4–16 mm. wide, glabrate or somewhat hirsute, the margins ciliate; upper stem leaves reduced, linear or lanceolate to ovate, the uppermost generally less than 15 mm. long, glandular-scabrous or more or less hairy or both; heads 1–6, cymose, the disks 10–20 mm. broad and 5–10 mm. high; phyllaries in two or three series of about equal length, linear, the outer ones mostly 0.7–1.1 mm. wide (in var. *viscidus* sometimes only 0.6 mm. wide), acuminate, glandular or viscid and often hirsute; ligules numerous, approximately 75–150, 8–15 mm. long and about 1 mm. wide, blue, rarely pink or white; pappus double, the outer setulose and sometimes very scanty. Meadows and open ground in the mountains, often at high altitudes. Arizona, New Mexico, Utah, Colorado, Wyoming, and the Black Hills of South Dakota.

6a. **Erigeron formosissimus** Greene var. **typicus** Cronquist, var. nov. *E. formosissimus* Greene, Bull. Torrey Club **25**: 121, as to type. 1898. *E. hirtuosus* Greene, Leafl. **2**: 209. 1912. *E. subasper* Greene, Leafl. **2**: 195. 1912. *E. fruticetorum* Rydb. Fl. Rocky Mts. 906. 1917.

Involucre glandular and more or less densely hirsute, the long hairs sometimes so numerous as to obscure the glands; basal leaves frequently acutish; uppermost leaves long-hairy or nearly glabrous, with strongly hirsute-ciliate margins, commonly not at all glandular; upper part of the stem glandular and with long spreading hairs. Range of the species.

6b. **Erigeron formosissimus** Greene var. **viscidus** (Rydb.) Cronquist, comb. nov. *E. grandiflorus* Nutt. Jour. Phila. Acad. **7**: 31. 1834. Not *E. grandiflorus* Hook. 1834. *E. eximius* Greene, Pittonia **3**: 295. March 29, 1898. See note under *E. superbus.* *E. viscidus* Rydb. Bull. Torrey Club **28**: 24. 1901. *E. Gulielmi* Greene, Leafl. **2**: 195. 1912. *E. iodanthus* Greene, Leafl. **2**: 209. 1912. *E. rubicundus* Greene, Leafl. **2**: 209. 1912. *E. scaberulus* Greene, Leafl. **2**: 212. 1912. *E. Smithii* Rydb. Bull. Torrey Club **32**: 125. 1905.

Involucre densely glandular, sometimes also with a few long hairs; basal leaves rarely if ever acutish; uppermost leaves glandular-scabrous, commonly without long hairs except for the ciliate margins; upper part of the stem glandular, with or without long spreading hairs. Range of the species.

Forms of *E. formosissimus* var. *typicus* are frequently rather tall, with the upper leaves comparatively little reduced, thus seemingly approaching *E. subtrinervis*. These may be distinguished from that species, however, by the comparatively wide phyllaries with mostly appressed tips.

7. ERIGERON GLABELLUS Nutt. Gen. Pl. **2**: 147. 1818.

Biennial or perennial herbs with simple or slightly branched caudices and fibrous root systems; stems erect, 1–5 (rarely 7) dm. high; herbage sparsely to densely hirsute or strigose with appressed or spreading hairs; basal and lowermost cauline leaves oblanceolate, entire or irregularly toothed, acute to obtuse or rarely rounded at the tips, tapering gradually to winged petioles or petioliform bases, the blade and petiole if present mostly 4–15 cm. long and 3–15 mm. wide; middle stem leaves linear or lanceolate, usually conspicuously smaller than the lower ones, often bract-like; heads 1–15, cymose, usually on long nearly naked peduncles, the disk 10–20 mm. broad, 6–13 mm. high; phyllaries in two or three series of about the same length, sometimes somewhat imbricated, linear, the outer ones mostly 0.5–0.9 mm. wide, acuminate, hirsute or strigose, not glandular, appressed; ligules numerous, about 125–175, 8–15 mm. long, about 1 mm. wide, blue or pink, less commonly white; pappus double, the outer setulose and sometimes very scanty. Meadows, prairies, and open ground; Alaska and Northwest Territory, south to Montana, Utah, South Dakota, and Wisconsin.

1. Pubescence appressed or closely ascending ..... a. subsp. *typicus*
1. Pubescence spreading ..... b. subsp. *pubescens*

7a. **Erigeron glabellus** Nutt. subsp. **typicus** Cronquist, subsp. nov. *E. asper* Nutt. Gen. Pl. **2**: 147. 1818. *E. glabellus* Nutt. Gen. Pl. **2**: 147. 1818. *E. oblanceolatus* Rydb. Bull. Torrey Club **24**: 294. 1897. *E. anicularum* Greene, Leafl. **2**: 215. 1912. *E. anicularum* Greene var. *latiusculus* Greene, Leafl. **2**: 216. 1912. *E. multicolor* Lunell, Am. Midl. Nat. **2**: 255. 1912. *E. obscurus* Lunell, Am. Midl. Nat. **2**: 256. 1912. *E. asper* Nutt. var. *appressus* Lunell, Am. Midl. Nat. **3**: 3. 1913. *E. oligodontus* Lunell var. *acuminatus* Lunell, Am. Midl. Nat. **3**: 4. 1913. *E. subcostatus* Lunell, Am. Midl. Nat. **3**: 5. 1913. *Tessenia glabella Lunell*, Am. Midl. Nat. **5**: 59. 1917.

Most of the names in the above list were transferred to *Tessenia* by Lunell in 1917.

Pubescence appressed or closely ascending, mostly short and fine; crosswalls of the hairs not at all conspicuous if present. Colorado, South Dakota, and Utah, north to southern Manitoba and Saskatchewan.

7b. **Erigeron glabellus** Nutt. subsp. **pubescens** (Hook.) Cronquist, comb. nov. *E. glabellus* Nutt. β *pubescens* Hook. Fl. Bor. Am. **2**: 19. 1834.

E. consobrinus Greene, Pittonia **3**: 186. 1897. *E. fraternus* Greene, Pittonia **3**: 162. 1897. Not *E. fraternus* Greene, Pittonia **2**: 169. 1891. *E. Drummondii* Greene, Pittonia **3**: 295. 1898. *E. Earlei* Rydb. Bull. Torrey Club **32**: 126. 1909. *E. abruptorum* Lunell, Am. Midl. Nat. **3**: 13. 1913. *E. anodontus* Lunell, Am. Midl. Nat. **3**: 6. 1913. *E. asper* Nutt. var. *subinteger* Lunell, Am. Midl. Nat. **3**: 143. 1913. *E. oligodontus* Lunell, Am. Midl. Nat. **3**: 4. 1913. *E. oxyodontus* Lunell, Am. Midl. Nat. **3**: 3. 1913. *E. procerus* Lunell, Am. Midl. Nat. **3**: 5. 1913. *Tessenia glabella* Lunell var. *subdiscoidea* Lunell, Am. Midl. Nat. **5**: 59. 1917.

Most of the names in the above list were transferred to *Tessenia* by Lunell in 1917.

Pubescence spreading, particularly on the stem, often long and coarse; cross-walls of the hairs often highly conspicuous. Alaska and Northwest Territory south to Montana, North Dakota, and Wisconsin; also in Colorado.

E. glabellus subsp. *pubescens* occurs quite commonly in the mountains of Colorado in the same general area that is occupied by subsp. *typicus*. The hypothesis is advanced that subsp. *pubescens*, the ancestral form of the species, migrated north across the plains after the retreating glaciers, giving rise to subsp. *typicus* somewhere in the early part of the migration. Some plants of subsp. *pubescens* remained in the central Rocky Mountains and moved upward in altitude as the climate warmed. These now persist as an island surrounded by plants of subsp. *typicus*.

Dr. Joel Lunell segregated a large number of "new species" from *E. glabellus*. Frequently both subspecies are represented in his type collections, as he worked in an area where the two merge. The reductions made here are based on his type sheets in the University of Minnesota herbarium.

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A TAXONOMIC REVISION OF THE GENUS HOLODISCUS (ROSACEAE)

ARLINE LEY

INTRODUCTION

The revision of the genus *Holodiscus* was suggested to me as a taxonomic problem by Dr. Philip A. Munz of Pomona College, to whom I wish to express the deepest gratitude for invaluable guidance and aid. I am also indebted to Mr. G. L. Wittrock of the New York Botanical Garden and to Miss Ruth Sanderson of the Gray Herbarium who have sent me important original descriptions of many species. I should like to thank those in charge of the following herbaria who have kindly loaned their material for this study:

California Academy of Sciences (CAS),
University of Michigan (MICH),
New York Botanical Garden (NY),
Pomona College (POM),
Santa Ana Botanical Garden (RSA),
University of California at Los Angeles (LA),
United States National Herbarium (US)—Mexican and South American specimens.

Abbreviations following the above names are those used in this paper in citation of specimens.

HISTORY OF THE GENUS

The plants now referred to the genus *Holodiscus* were originally included in the genus *Spiraea*. The type species of the genus, collected in New Granada (now Colombia) by Mutis, was described as *Spiraea argentea* by Linnaeus f., Suppl., 261 (1781). In 1836 Rafinesque applied the name *Schizonotus* to the species *Spiraea discolor* Pursh (Fl. Am. **1**: 342. 1814). In New Fl. **3**: 74 (1836) he stated that he "adopted the Genus and name *Schizonotus* upon the suggestion of Lindley," but he did not know how the name "split back" applied "unless the capsules open outside." In Sylva Tell., 152 (1838) he applied the name *Sericotheca* (from the Latin, "silky" and "case," referring to the hairy carpels) based on the species *Spiraea argentea*. The name *Schizonotus* Lindl. had already been established as a synonym for *Spiraea Lindleyana* Wall. by Lindley (ex Wall. Cat. n. 703. 1830), but had become obsolete. Rafinesque took the name and applied it here.

The name *Holodiscus* (from the Greek, "whole" and "disk," referring to the entire disk of the flower) was first applied to this group by Koch,

Dendr. **1**: 309 (1869), who made it a section under *Spiraea*, based on *Spiraea ariaefolia* Smith (in Rees, Cycl. **33**: no. 16. 1819). Maximowicz, Acta Hort. Petrop. **6**: 253 (1879), used the name *Holodiscus* in the tribe Potentilleae. It was later placed in a special tribe, Holodisceae, by Focke in Engler and Prantl, Nat. Pfl. **3** (3) : 18 (1894). Focke separated the genus from *Spiraea* because of the one-seeded indehiscent fruit. He recognized two species, *H. discolor* (Pursh) Maxim. and *H. argenteus* (L.f.) Maxim.

In 1891 O. Kuntze, Rev. Gen. **1**: 225, again used the name *Schizonotus* for the genus and recognized only one species, *Schizonotus argenteus* (L.f.) Kuntze, with ten varieties. Schneider, Handb. Laubh. **1**: 495 (1905), in his treatment of the genus placed it under the subfamily Holodisceae, calling the genus *Holodiscus*. He was not satisfied with Kuntze's treatment of the group and recognized five species which he divided into two main types: those of the United States, and those of Mexico and South America. His five species included: *H. discolor*, *H. dumosus*, *H. australis*, *H. fissus*, and *H. argenteus*.

The genus was last revised as a whole by Rydberg (N. Am. Fl. **22**: 261. 1908) who revived the name *Sericotheca* and placed the genus under the tribe Holodisceae. He recognized fourteen species: 9 United States and 5 Mexican and South American species. *Schizonotus* Raf. has now been rejected, and *Holodiscus* Maxim. is placed in the Nomina Conservanda of the International Rules of Botanical Nomenclature, 98 (1935).

CHARACTERS USED IN CLASSIFICATION

The species of the genus *Holodiscus* are found to intergrade to some extent in most cases. The most consistent character used in classification is the leaves. The size, shape, pubescence, and glandular condition of the leaves, as well as the nature of the petiole and teeth, are the important key characters in the genus. While these intergrade to varying degrees, the groups can usually be readily separated on this basis. The length and shape of the sepals are not consistent throughout, although Rydberg used these to separate certain species. In the same way the nature of the inflorescence is not consistent enough to be used in distinguishing species. The pubescence on the backs of the petals proves to be denser in some species and is a fairly reliable character in separating the United States forms from those to the south.

In general, two principal groups might be separated: one ranging from British Columbia through western United States to northern Mexico; and another, from central Mexico south to Colombia. The southern group is distinct in having long, pointed mucros on the teeth which are often bent, in the greater length of the leaf-blades as compared to the width, and in the greater pubescence on the outer surface of the petals.

DESCRIPTION OF THE GENUS

Holodiscus Maxim. Acta Hort. Petrop. **6**: 253. 1879; Kuntze, Rev. Gen. **1**: 225. 1891; Engler & Prantl, Nat. Pfl. **3**(3): 18. 1894; Schneider, Handb. Laubholzk. **1**: 495. 1905.

Spiraea § *Holodiscus* K. Koch, Dendr. **1**: 309. 1869.

Spiraea § *Spiraria*, Sèr. in DC. Prod. **2**: 544, in part. 1825.

Spiraea Endlicher, Gen. Pl. 1247, in part. 1840; Benth. & Hooker, Gen. Pl. **1**(2): 611. 1865; Brewer & Wats. Bot. Calif. **1**: 170. 1876.

Schizonotus Raf. New Fl. **3**: 74. 1836. Not *Schizonotus* Lindl. 1830; Piper, Contr. U. S. Nat. Herb. **11**: 330. 1906.

Sericotheca Raf. Sylva Tell. 152. 1838; Rydb. N. Am. Fl. **22**: 261. 1908.

Sepals 5, 3-nerved, valvate in the bud, erect in fruit. Petals 5, short-clawed or rounded. Hypanthium saucer-shaped, adnate to base of calyx; disk entire. Stamens usually 20, inserted on disk with 3 stamens opposite each petal, one opposite each sepal; anthers didymous. Pistils 5, distinct, alternate with sepals, villous, inserted on center of disk, sessile; styles terminal; ovules 2, collateral, pendulous. Fruit indehiscent, one-seeded, enclosed in the calyx, short-stipitate, laterally flattened, villous, membranaceous, caducous, convex on lower suture. Seeds pendulous, broadly oblong, with double coat, thin endosperm; embryo with superior radicle and ovate cotyledons. Shrubs or small trees, spreading, to 7 m. tall, with alternate, simple, toothed leaves; stipules lacking. Inflorescence terminal with whitish or pinkish flowers, villous, racemose or paniculate.

TYPE SPECIES: *H. argenteus* (L.f.) Maxim. The genus is distributed from Canada south throughout western United States to South America.

KEY TO SPECIES

A. Teeth ending in a short, straight, rounded mucro; petals with a few long hairs at outer base; stamens longer than sepals.

B. Leaf-blades toothed along sides below middle, elliptic to orbicular, not obovate.

C. Leaves elliptic to elliptic-ovate or ovate, longer than broad, with 3–6 teeth on each side, usually deeply toothed, glabrous or with a scattered pubescence above.

D. Leaves not decurrent on petiole but contracted at base forming a distinct petiole, teeth usually divided 3–6 times except in var. *delnortensis*. Coastal British Columbia to Southern Calif. ..... 1. *H. discolor.*

DD. Leaves decurrent on petiole, teeth usually simple, rarely doubly divided.

E. Leaves deeply toothed, teeth narrow, leaf blades narrowly cuneate at base. Wyoming to Arizona and Chihuahua ..... 2. *H. dumosus.*

EE. Leaves not deeply toothed, teeth broad and rounded, leaf blades very broad at base, abruptly contracted. Valley of Mexico ..... 3. *H. pachydiscus.*

CC. Leaves broadly ovate to orbicular, almost as broad as long, with 3–4 teeth on each side, not deeply toothed, pubescent to villous above, blades abruptly contracted, forming a short winged petiole. Mts. of California ..... 4. *H. Boursieri.*

BB. Leaf-blades toothed at top, rarely to middle, obovate to spatulate. Mts. from Oregon to Baja California ..... 5. *H. microphyllus.*

AA. Teeth ending in a long, pointed, often bent mucro; petals with a scattered, often dense pubescence on outer side; stamens not longer than sepals.

B. Leaf-blades acute at apex, linear to lanceolate, tomentose to villous beneath.

C. Leaf-blades 4–5 times as long as wide, almost entire, the teeth scarcely noticeable. Orizaba ..... 6. *H. orizabae.*

CC. Leaf-blades 2–3 times as long as wide, coarsely toothed. Michoacán and Guerrero (Mexico) to Guatemala ..... 7. *H. fissus.*

BB. Leaf-blades obtuse to rounded at apex, oblanceolate to obovate, white silky beneath. Oaxaca (Mexico) to Colombia ..... 8. *H. argenteus.*

TREATMENT OF SPECIES

1. HOLODISCUS DISCOLOR (Pursh) Maxim. Acta Hort. Petrop. **6**: 254. 1879.

A tall spreading shrub, 1.5–6 m. tall; bark of older branches dark-reddish to chestnut brown, becoming dark gray and exfoliating; young twigs light, straw-colored, pubescent, even villous; internodes about one-half the length of leaves; leaf-blades ovate to ovate-elliptic or -oblong, either truncate or cuneate at base, not decurrent on the distinct petiole, the apex rounded to obtuse, teeth deep, broad and round, ending in a short mucro, usually with 4–6 teeth on each side, each tooth divided 1–6 times except in var. *delnortensis,* the leaves gray-green to green above, sparingly pubescent, usually paler beneath, pubescent to villous or tomentose, the leaf-blades 3.0–8.0 cm. long and 2–7 cm. wide; petioles 0.5–2.5 cm. long; inflorescence spreading, dense, very compound, villous, 5–25 cm. long, and 5–25 cm. wide; pedicels 1.5–3.0 cm. long, with linear bracts 1 mm. long; sepals triangular-ovate to elliptic-ovate, acute to obtuse at apex, 1.5–2.0 mm. long; petals oval, 2 mm. long, with several hairs on the outer base; stamens longer than sepals; carpels very villous, up to 1.5 mm. long; styles up to 1 mm. long; achenes with straight upper edge and very much convex lower edge.

KEY TO VARIETIES

Leaf-blades at least 4.5 cm. long, 3–7 toothed on either edge, and with short pubescence on lower surface. British Columbia to Montana and Southern California ..... 1a. *H. discolor* var. *typicus.*

Leaf-blades less than 4.5 cm. long, 2–4 toothed on either edge, often with many long hairs beneath.

Teeth of leaves compound, leaves grayish beneath, petioles 5–8 mm. long. Southern Oregon to Southern California ..... 1b. *H. discolor* var. *franciscanus.*

Teeth of leaves usually simple, leaves whitish beneath, petioles 6–12 mm. long. Crater Lake, Oregon, to Del Norte Co., California. 1c. *H. discolor* var. *delnortensis.*

1a. H. DISCOLOR var. **typicus** Ley, var. nov.

Spiraea discolor Pursh, Fl. Am. 342. 1814; *Schizonotus discolor* Raf. New Fl. 3: 75. 1836; *Holodiscus discolor* Maxim. Acta Hort. Petrop. 6: 254. 1879; *Schizonotus argenteus* var. *discolor* Kuntze, Rev. Gen. 1: 225. 1891; *Sericotheca discolor Rydb.* N. Am. Fl. 22: 262. 1908; *Spiraea ariaefolia* Smith, in Rees' Cycl. 33: no. 16. 1819; *Spiraea discolor* var. *ariaefolia* S. Wats. Bot. Calif. 1: 170. 1876; *Schizonotus argenteus* var. *ariaefolius* Kuntze, Rev. Gen. 1: 225. 1891; *Schizonotus ariaefolius* Greene, Fl. Fran. 58, in part. 1891; *Schizonotus discolor* var. *Purshianus* Rehder in Bailey, Cycl. Am. Hort. 4: 1627. 1902.

Illustration: Figure 8.

Leaf-blades broadly ovate with a truncate base, to ovate-elliptic with cuneate base, villous-pubescent to tomentose beneath, 4.5–7 (10) cm. long, 2.5–8 cm. wide, the petioles 0.7–2 cm. long; inflorescence spreading, 7–20 cm. long, 5–20 cm. wide.

There has been a great deal of confusion concerning the species *Spiraea ariaefolia* Sm., *S. discolor* Pursh and *S. dumosa* Nutt. By some *S. ariaefolia* is treated as the coastal form, and *S. discolor* Pursh and *S. dumosa* Nutt, as the Rocky Mountain form. Other investigators feel that *S. ariaefolia* Sm. and *S. discolor* Pursh are in the same species, and the *S. dumosa* Nutt. is different. From the literature and specimens reviewed, it would seem that the Rocky Mountain material is very different from the specimens of the northwest. I have not seen type material of *S. dumosa* Nutt., but from descriptions of Torrey (Ann. Lyc. N. Y. **2**: 195. 1827), Torrey and Gray (Fl. N. Am. **1**: 416. 1840), and Hooker (Lond. Jour. Bot. **6**: 217. 1847), I believe it to be entirely different from *S. ariaefolia* Sm. and *S. discolor* Pursh. These two are here considered the same form and are included under *H. discolor* var. *typicus.*

This variety cannot be clearly distinguished in all cases from var. *franciscanus.* The two intergrade in the size and thickness of the leaves in the counties about San Francisco Bay, as for example do the following specimens from that region: Leona, Alameda Co., *Michener and Bioletti in 1892* (NY); Oakland Hills, near San Francisco, Alameda Co., *Torrey 133* (NY); and Los Troncos Creek, San Mateo Co., *Berry in 1909* (POM). These specimens resemble var. *franciscanus* in leaf form, but are 4.5 cm. long. There are a few forms which might be included with var. *franciscanus* because of their small leaf size, such as the specimens: MONTANA: Bigfork, Flathead Lake, Flathead Co., *Jones 8300* (POM); and Flathead Valley, *MacDougal 757* (NY). B.C.: Goldstream, Vancouver Is., *Macoun in 1887* (NY). WASHINGTON: Friday Harbor, San Juan Co., *Heller 970* (LA, NY); Tacoma, Pierce Co., *Millis in 1883* (NY). OREGON: unknown locality, *Spalding* (NY), Mt. Hood, *Jones in 1897* (POM); the Dalles, Wasco Co., *Jones in 1897* (POM). However, I feel that these are exceptions and should be included under var. *typicus* because of the very broad inflorescence and the thin leaves in most cases, as well as because of their distribution.

TYPE collected by Lewis on the banks of the Kooskoosky, Idaho. Range, along streams, on rocky hillsides or in open woods, between 50 and 4500 feet, from B. C. to Mont. and Coastal S. Calif. *Representative material:* MONTANA: Hitchcock 1671, 1886. IDAHO: *MacDougal 176, Leiberg 1310, Aiton 6171, Sandberg 583, M. E. Jones 6285, Clark 171.* B. C.: *Eastwood 9909, Macoun 34817, 34818.* WASHINGTON: *Elmer 2522, Heller 4025, Allen 2, Thompson 9818.* OREGON: *Menzies,* part of type collection of *ariaefolia* (NY), *Sheldon 10977, Jones 4210.* CALIFORNIA: *Heller 7514, Hoffman 645, no. 9, Eastwood 6464, Munz 2218, Abrams 4723.*

1b. H. DISCOLOR var. FRANCISCANUS (Rydb.) Jepson, Fl. Calif. **2**: 166. 1936.

Sericotheca franciscana Rydb., N. Am. Fl. **22**: 262. 1908; *Holodiscus franciscanus* Rehder, Jour. Arnold Arb. **1**: 260. 1920.

Illustration: Figure 9.

Leaf-blades thick, usually broadly ovate with truncate base and rounded

apex, villous beneath, usually 3–4.25 cm. long, 2–3 cm. wide, petioles 0.5–0.8 cm. long; inflorescence 7–12 (18) cm. long, 6–12 cm. wide.

TYPE: San Leandro, Alameda Co., Calif., *L. M. Underwood in 1888* (NY). Range, on open hillsides or along streams, between 300 and 2900 ft., S. Ore. to Orange Co., Calif. *Representative material:* OREGON: *Heller 13070, 12634.* CALIFORNIA: *Butler 1645, Heller 11545, 12362, 5729, Abrams 5920, Jones 3579, Keck 1795, Elmer 4274, Stark 2248.*

As has been noted above under the variety *typicus*, there are a few plants found about San Francisco Bay which intergrade with that variety in leaf-size, for example: *Eastwood 4733, Michener & Bioletti* in 1892, *Carruth* in 1901. Because of their thick leaves they are placed under var. *franciscanus*, although rather large.

1c. H. DISCOLOR var. **delnortensis** Ley, var. nov.

Folia ovata cum basi cuneato, supra grisea et pubescentia, infra tomentosa et alba, simplice dentata; laminis foliorum 1.5–3.5 cm. longis, 1–2 cm. latis; petiolis 0.6–1.2 cm. longis; inflorescentia 6–14 cm. longa, 3–7 cm. lata.

Illustration: Figure 10.

TYPE: Darlingtonia, Smith River, Del Norte Co., Calif., *H. E. & S. T. Parks 24019*, POM. no. 257430; isotypes RAS, NY, CAS. Range from Crater Lake, Oregon to Del Norte Co., California; represented by: OREGON: *Jones 7723, 7752.* CALIFORNIA: *Abrams 8436, Wolf 864, 9127, Eastwood 12195, 2131.*

This variety is very close to *H. discolor* var. *franciscanus*, but differs in the very white appearance of the undersides of the leaves and in having simple teeth. There is a tendency for this group to have a longer petiole as compared to the length of the leaf blade than in the other two varieties. The shape of the leaf is very characteristic, the leaf-blade being narrow at the top, broad near the base, and becoming cuneate.

2. HOLODISCUS DUMOSUS (Nutt.) Heller, Cat. N. Am. Pl, 4. 1898.

A spreading shrub, 1–3 m. tall; bark of older twigs dark red, later becoming dark gray and exfoliating; young twigs light, often straw-colored, very villous, the internodes from much less than, up to length of leaves; leaf-blades elliptic or elliptic-ovate with cuneate base decurrent on petiole, the apex rounded to obtuse, the teeth rather deep, usually simple, sometimes double, ending in a short, blunt mucro, mostly with 3–6 teeth on each side, the leaves gray-green above and glabrous, or slightly pubescent between veins, either whitish beneath and both tomentose and villous with long silky hairs especially along veins, or sparingly pubescent beneath with gland droplets between veins, the leaf-blades 1–3.5 (5) cm. long and 0.5–2 cm. wide, the petioles 0.2–1 (1.4) cm. long; inflorescence with spreading branches, compound especially in lower part, densely villous, 5–20 cm. long, 3–10 cm. wide; pedicels 2–3 mm. long, subtended by linear bracts scarcely 1 mm. long; sepals triangular-ovate, 1.5–2 mm. long; petals oval, rarely with several long hairs at base beneath, 2 mm. long; stamens slightly longer than sepals; carpels very villous, 1 mm. long; styles 1 mm. or less, achenes with straight upper edge and very much convex lower edge.

KEY TO VARIETIES

Leaf-blades pubescent to villous, not glandular beneath.

Leaf-blades pubescent beneath, rarely villous, 1–2 cm. long, about twice as long as wide; inflorescence small and spreading. Wyoming to eastern Utah and Colorado ..... 2a. *H. dumosus* var. *typicus.*

Leaf-blades very villous beneath, 2.3–5 cm. long, more than twice as long as wide; inflorescence large and spreading. Southeastern Colorado to Arizona and Chihuahua ..... 2b. *H. dumosus* var. *australis*.

Leaf-blades scarcely pubescent beneath with long hairs along veins and with gland droplets between veins, 1.5–2.5 cm. long, about twice as long as wide. San Luis Potosí, Mexico ..... 2c. *H. dumosus* var. *Schaffneri*.

2a. H. DUMOSUS var. **typicus** Ley, var. nov.

Spiraea dumosa Nutt. ex Torr. & Gray, Fl. N. Am. 1: 416, as syn. 1840; Hooker, London Jour. Bot. 6: 217. 1847; *Spiraea discolor* var. *dumosa* S. Wats. Bot. Calif. 1: 170, in part. 1876; *Schizonotus argenteus* var. *dumosus* Kuntze, Rev. Gen. 1: 226, in part. 1891; *Holodiscus discolor* var. *dumosus* Dippel, Handb. Laubh. 3: 508. 1893; *Schizonotus dumosus* Koehne, Deuts. Dendr. 265. 1893; *Holodiscus dumosus* Heller, Cat. N. Am. Pl. 4. 1898; *Schizonotus discolor* var. *dumosus* Rehder, Cycl. Am. Hort. 4: 1629, in part. 1902; *Sericotheca dumosa* Rydb. N. Am. Fl. 22: 263. 1908.

Illustration: Figure 5.

Frequently a low shrub about 1 meter high; leaf-blades usually less than 2 cm. long and about half as wide, usually slightly villous, teeth most often rounded, not usually pointed; inflorescence branched, 5–12 cm. long, 2–7 cm. wide.

TYPE collected by Nuttall, stony and sandy places of the Platte River. Growing among rocks or brush, between 2300 and 9400 ft., Wyo. and Colo. to eastern Utah and northern Arizona. *Representative material:* WYOMING: *Nelson 657, 9247, 7481.* UTAH: *Goodding 1271, Rydberg & Garrett 9468.* COLORADO: *Palmer 38122, Osterhout 2121, Patterson 22, Baker 264.* ARIZONA: *Toumey* in 1892, *Osterhout 6986, Eastwood 5889, Rusby 588.*

2b. H. DUMOSUS var. **australis** (Heller) Ley, comb. nov.

Holodiscus australis Heller, Bull. Torrey Club 25: 194, *pl. 338.* 1898.

Illustration: Figure 4.

Shrub 2–3 m. high; leaf-blades usually densely villous and tomentose beneath, 2–3 (5) cm. long, less than half as wide, the teeth usually drawn out and pointed; inflorescence spreading, 6–20 cm. long, 3–6 cm. wide.

Type collection, from Santa Fé Canyon, 9 mi. east of Santa Fé, New Mexico, *Heller 3840.* Growing in dry rocky places between 7000 and 11000 ft., southeastern Colorado to Arizona, Texas, and Chihuahua. *Representative collections:* COLORADO: *Clements 127, Clokey 3794, Rollins 1841.* ARIZONA: *Jones 3960, Wolf 3151, Peebles & Harrison 2255, Blumer 1281.* NEW MEXICO: *Wolf 2714, 2842, Metcalfe 250, 1171, Wooton 284.* TEXAS: *Moore & Steyermark 3572, Ferris & Duncan 2530.* CHIHUAHUA: *Pringle 7834, Goldman 1414, Nelson 4874.*

The following specimens have small leaf-blades, but the slender narrow leaf and pointed teeth would indicate that they belong in this group: ARIZONA: *Griffiths & Thornber 165.* NEW MEXICO: *Diehl 452.* TEXAS: *Mueller 8288.* CHIHUAHUA: *Barber & Townsend 144, 147, Nelson 6150, Mueller 1242.*

Rydberg (N. Am. Fl. **22**: 263. 1908) does not separate *australis* from the more northern material and merely recognizes it as "the form with thinner, more acutish leaf-blades and more simple toothing." As a whole it differs in leaf-size, breadth-to-length ratio, toothing and length of sepals.

2c. H. DUMOSUS var. **Schaffneri** (Rydb.) Ley, comb. nov.

Sericotheca Schaffneri Rydb., N. Am. Fl. 22: 264. 1908; *Holodiscus Schaffneri* Standley, Pub. Field Mus. Bot. 4: 210. 1929.

Leaf-blades scarcely pubescent beneath with long hairs on veins and with gland-droplets between veins, the teeth broad and rather rounded; leaf-

blades 1.5–4.5 cm. long, about half as wide; inflorescence 4–8 cm. long, 3–7 cm. wide.

TYPE: San Luis Potosí, Mexico, *Schaffner 457*. Known only from the type region, from such collections as *Parry & Palmer 223, Mueller 2222, Lundell 5391*.

3. HOLODISCUS PACHYDISCUS (Rydb.) Standley, Pub. Field Mus. Bot. **4**: 210. 1929.

Sericotheca pachydisca Rydb., N. Am. Fl. 22: 263. 1908.

Illustration: Figure 7.

Older branches dark-gray with exfoliating bark, angled; young twigs light reddish-brown, pubescent, angled, internodes about one-half length of leaves; leaf-blades broadly ovate, more or less abruptly contracted at base with a short winged petiole, the apex obtuse, many-toothed, the teeth very broad and rounded, simple, ending in a short, blunt mucro, 3–4 on each side, the leaves pubescent above, grayish and villous beneath, the blades 1.5–3 cm. long, 0.8–2.5 cm. wide; petioles 2–3 mm. long; inflorescence spreading, compound, with a short dense pubescence, 3.5–15 cm. long, 3–15 cm. wide; pedicels 2–3 mm. long, with three linear bracts up to 2 mm. long; sepals triangular-ovate, glabrous within, acute at apex, 1.5 mm. long; petals elliptical, 1.5–2 mm. long; stamens as long as sepals, inserted on a thick fleshy hypanthium; carpels very villous.

TYPE: Valle de Mexico, Tacuboya, *Bourgeau 267* (US. Photo of type, NY). Known only from a single collection.

4. HOLODISCUS BOURSIERI (Carr.) Rehder in Bailey, Cycl. Hort. 1498. 1915.

Spiraea Boursieri Carr. Rév. Hort. 1859: 520, *f. 108*. 1859; *Sericotheca Boursieri* Rydb. N. Am. Fl. 22: 263. 1908; *Holodiscus saxicola* Heller, Muhlenbergia 1: 41, 1904; *Sericotheca saxicola* Rydb. N. Am. Fl. 22: 263. 1908; *Sericotheca obovata* Rydb. N. Am. Fl. 22: 264. 1908.

Illustration: Figure 6.

A low shrub up to 1 m. high; bark of older branches dark reddish, becoming dark gray, exfoliating; young twigs straw-colored, often angled, short-pubescent to villous-pubescent, internodes from half as long as to as long as leaves; leaf-blades broadly obovate to orbicular, the base sometimes cuneate, more or less abruptly contracted, forming a short, winged petiole, the apex broad and rounded, many-toothed, the teeth broad and rounded, not deep, ending in a very short, blunt mucro, usually 3–4 teeth on each side extending at least to middle of leaf-blade, the leaves green or gray-green above, finely to villous-pubescent, grayish or whitish beneath, villous to villous-tomentose, often glandular, the leaf-blades 1–3 cm. long, 1–2.5 cm. wide; petioles 2–3 mm. long; inflorescence narrow to spreading, villous, 2.5–8 cm. long, 2.5–8 cm. wide; pedicels 1–2 mm. long, with three bracts, linear to narrowly lanceolate, 1 mm. long; sepals triangular-ovate with acute apex, 1.5–2 mm. long; petals oval, 2 mm. long, with a few long hairs at outer base; stamens longer than sepals; carpels villous, 1.5 mm. long, styles 1 mm. long, achenes with straight upper edge and very convex lower edge.

Type locality, California. Growing among rocks, between 4600 and 8000 feet, in the mountains of California and adjacent Nevada. *Representative specimens:* CALIFORNIA: *Train 250, Howell 13493, Hitchcock & Martin 5357, Jones 2506, Heller 14451, 7160* (type no. of *H. saxicola*), *12896, Crum 2078, Johnston 1566, Everett 7221, Wolf 5390*. NEVADA: *Greene 1431*. Intermediate between *H. saxicola* and *Boursieri*, as separated by

some authors, are *Hansen 234, Bracelin 913, Eastwood 249;* for this reason I cannot maintain two separate entities. Although I have not seen the type of *Spiraea Boursieri* Carr., the figure given in the original description is well matched by *Heller 12896, Everett 7221, Johnston 1566.*

5. HOLODISCUS MICROPHYLLUS Rydberg, Bull. Torrey Club **31**: 559. 1904.

Low spreading shrub, 15 cm. to 2 m. high; bark of older twigs dark red, later becoming dark gray and exfoliating; young twigs reddish tan to light tan, glabrescent with gland droplets to villous-pubescent, the internodes from one-half as long as to as long as leaves; leaves in fascicles of 1–8, obovate to spatulate with cuneate base decurrent on petiole, the apex rounded, many-toothed, the teeth usually small, broad, and rounded, often ending in a short, blunt mucro, 2–3 on each side, the leaf-blades toothed only above middle, light green or gray green above, glabrescent to villous above, glabrescent with gland droplets to villous-tomentose beneath, white-silky beneath in some, the leaf-blades 0.5–1.75 cm. long, rarely 2 cm. long, 0.3–1 cm. wide; petioles 1–2 mm. long; inflorescence usually narrow and compact, rarely compound, villous, 2.5–3.5 cm. long, 1–3 cm. wide; pedicels 1–3 mm. long with linear bracts, 1 (rarely 2) mm. long; sepals narrow, triangular-elliptic with acute apex, 1–1.5 mm. long; petals oval to elliptic, 1.5–2 mm. long, glabrous beneath or with a few long hairs at outer base; stamens longer than sepals; carpels villous, 1 mm. long, styles 1 mm. long, achenes with straight upper edge and convex lower edge.

KEY TO VARIETIES

Leaf-blades pubescent to villous beneath, with hairs masking gland-droplets if these are present, often pubescent above.

Leaf-blades villous beneath, finely to densely pubescent above. Idaho, to California, and Colorado ..... 5a. *H. microphyllus* var. *typicus.*

Leaf-blades densely white-silky beneath, villous above. Clark Co., Nevada, Arizona, and San Jacinto Mts., California, Lower California. 5b. *H. microphyllus* var. *sericeus.*

Leaf-blades glabrescent to glabrous beneath with evident gland-droplets between veins, glabrescent or with a scattered pubescence above. Mts. from Oregon and California to Utah ..... 5c. *H. microphyllus* var. *glabrescens.*

5a. H. MICROPHYLLUS var. **typicus** Ley, var. nov.

Holodscus microphyllus Rydb. Bull. Torrey Club **31**: 559. 1904; *Sericotheca microphylla* Rydb. N. Am. Fl. **22**: 264. 1908; *Holodiscus discolor* var. *microphyllus* Jepson Fl. of Calif. 2: 166. 1936; *Sericotheca concolor* Rydb. N. Am. Fl. **22**: 264. 1908.

Illustration: Figure 1.

Leaf-blades pubescent to villous above, villous beneath, 0.5–2 cm. long, 0.3–1.2 cm. wide; inflorescence 3.5–9 cm. long, 1.5–7 cm. wide.

TYPE from Alta, Wasatch Mts., Utah, based on *Jones 1142* (NY, POM); range from California to Idaho and western Colorado. *Representative collections:* CALIFORNIA: *Heller 12135, Bracelin 888, Grant 1134, Eastwood 4332, Crafts 625, Munz 14819, 7625, Wolf 1699, 7644, 7649, Johnston 1696.* NEVADA: *Heller 10353, 9542, Duran 3104.* UTAH: *Eastwood 7705, Jones 5531.* COLORADO: *Baker, Earle & Tracy 8631.* ARIZONA: *Jones 6056.*

5b. H. MICROPHYLLUS var. **sericeus** Ley, var. nov.

Laminae foliorum supra villosae, infra albido-sericeae, 0.5–2 cm. longae, 0.4–1 cm. latae; inflorescentia 3–6 cm. longa, 1–4 cm. lata.

TYPE: Griffiths Mine, bottom of rocky ravine, Clark Co., Nevada, *Clokey 7969* (POM 257589; isotypes NY, RAS). Ranging from southern Nevada to Lower California. Material seen: NEVADA: Potosi Mt., *Jaeger* in 1930 (POM); *Heller 11006, Clokey 7556, 7138, 5507*. ARIZONA: Huachuca Mts., *Hilend* in 1931 (LA). CALIFORNIA: San Jacinto Mts., *Jaeger* in 1921 (POM). LOWER CALIFORNIA: *Wiggins & Demaree 5037, Goldman 1222*.

This variety might be confused with forms of *typicus* having densely villous leaves, but is more silvery beneath and with a greater contrast between pubescence on the upper and lower surfaces than in *typicus*, which is almost equally villous on both surfaces.

5c. H. MICROPHYLLUS var. **glabrescens** (Greenman) Ley, comb. nov.

Spiraea discolor var. *glabrescens* Greenman, Erythea **7**: 116. 1899; *Holodiscus glabrescens* Heller, Muhlenbergia **1**: 40. 1904; *Sericotheca glabrescens* Rydb. N. Am. Fl. **22**: 264. 1908; *H. discolor* var. *glabrescens* Jepson, Man. Fl. Pls. Calif. 479. 1925.

Leaf-blades glabrescent to glabrous above, glabrescent to glabrous beneath with many gland droplets between veins, 0.5–2 cm. long, 0.2–1.5 cm. wide; inflorescence 3–10 cm. long, 1–7 cm. wide.

TYPE from Stein's Mt., Oregon, *Cusick 1253* (NY); ranging through mountains of Oregon and California to Utah. *Representative numbers:* OREGON: *Cusick 2716, 1968, Hitchcock 4908, Abrams 9600, Thompson 12195*. CALIFORNIA: *Copeland, 375, 3784, Heller 11667, 11730, Cooke 11505*. UTAH: *Leonard 129, Eastwood & Howell 7169, Cottam 4535*.

In inflorescence, habit, leaf-size and -shape, this variety resembles var. *typicus;* it differs in the glabrescence of the leaves and the evident gland-droplets beneath.

6. **Holodiscus orizabae** Ley, sp. nov.

Illustration: Figure 2.

Rami subrubentes ad grisei, decorticantes; ramulis angulatis, villosis, internodiis plus quam dimidio longitudinis foliorum; laminis foliorum lanceo-ellipticis, angustissimis, cum base cuneato, in petiolis decurrentibus, apice acuto in mucro longissimo terminando, foliis subintegris, dentibus obscuris, mucronatis, tres utrimque, laminis foliorum in superficie superiore glabris vel pubescentibus, inferiore tomentoso-villosis, 2–3 cm. longis, 0.6–1 cm. latis; inflorescentia ampla, composita, 6–10 cm. longa, 4–8 cm. lata; pedicellis 0.3–0.5 cm. longis cum tres bracteis lanceolatis, 2–3 mm. longis; sepalis late triangulo-ovatis, ad apicem acutis, 2 mm. longis; petalis late ovatis ad orbiculatis, infra pubescentibus, in nervo mediano sericeis, 2 mm. longis, stylis 1 mm. longis, acheniis cum margine superiore leviter curvata et inferiore gibbissima.

TYPE: Vaquería de Jacal, Pico de Orizaba, Mexico, 10–11000 ft. *Liebmann 1670* (US, 1012847; isotypes, NY). Known only from the type collection.

The very narrow leaves of this species set it apart from any other form, and it seems advisable to recognize it as a distinct species. It corresponds in leaf-shape to the description in O. Kuntze's key (Rev. Gen. **1**: 226. 1891) of *Schizonotus argenteus* var. *angustissimus*. However, his description is very short and no specimens were cited by him. As I have not seen any specimens of this species annotated by him, I cannot with any degree of certainty designate this as the form to which he refers.

7. HOLODISCUS FISSUS (Lindl.) Schneider, Ill. Handb. Laubh. **1**: 495. 1905.

Spiraea fissa, Lindl., Bot. Reg. 2, misc., 73. 1840; 28, Misc., 1. 1842; *Schizonotus argenteus* var. *fissus* Kuntze, Rev. Gen. **1**: 226. 1891; *Schizonotus discolor* var. *fissus*

Rehder in Bailey, Cycl. Am. Hort. 1627. 1902; *Sericotheca fissa* Rydb. N. Am. Fl. 22: 265. 1908; *Spiraea argentea* Benth. Pl. Hartw. 82. 1841. Not *S. argentea* L. f. 1781. *Holodiscus argenteus* var. *bifrons* Focke, Bot. Gaz. **18**: 200. 1893; *Holodiscus Loeseneri* Dammer, Repert. Sp. Nov. **25**: 385. 1919.

Illustration: Figure 11.

Slender shrub 2–3.5 m. high; branches angled, more deeply ribbed in younger twigs, older branches dark red to dark gray, exfoliating; young twigs tan to light reddish-brown, with a short, dense pubescence, sometimes villous, the internodes $\frac{1}{4}$ to $\frac{1}{2}$ length of leaf; leaf-blades lanceolate to oval, cuneate at base, decurrent on petiole, acute to acuminate at apex, ending in a sharp mucro, the teeth conspicuous, usually ending in a long, sharp mucro, frequently bent, 5–9 teeth on each side with many small teeth near apex, the leaf-blades glabrous above or rarely with a scattered pubescence in young leaves, with a short, dense pubescence beneath, often villous, particularly along veins, 2.5–8 cm. long, 1–4 cm. wide; petioles 0.5–1.5 cm. long; inflorescence sparse, spreading, villous, 9–20 cm. long, 5–15 cm. wide; pedicels 2–3 mm. long with lanceolate bracts, these 1–3 mm. long, up to 1 mm. wide; sepals triangular with acute apex, 1–2 mm. long; petals oval to orbicular with fine pubescence scattered over back, particularly along veins, 2 mm. long; carpels villous, 1–2 mm. long; styles 1–2 mm. long; achenes with slightly curved upper edge and convex lower edge.

TYPE collected by Hartweg in Mexico. Range, southern Mexico to Guatemala. *Material seen:* MEXICO—MICHOACÁN: *Nelson 6583* (NY, US). GUERRERO: *E. Nelson 2210* (NY, US). OAXACA: *Smith 822* (US), *Camp 2637* (NY). CHIAPAS: *Seler 2156* (CAS, US), *Seler 2238* (US; type collection of *H. Loeseneri*), *Matuda 2580* (NY, MICH), *Matuda 5183, 0404* (MICH). GUATEMALA—QUICHÉ: *Heyde & Lux 3034* (NY, US; type collection of *H. argenteus* var. *bifrons* Focke). HUEHUETENANGO: *E. Nelson 3666a* (US)), *Salas 470* (US). CHIMALTENANGO: *Hartweg 575* (NY). The specimen from San Juan Atitlán, Dept. Huehuetenango, *Skutch 1179* (NY), is very small-leaved, but the acute apex and the shape of the leaf would seem to place it with *H. fissus*.

8. HOLODISCUS ARGENTEUS (L.f.) Maxim., Acta Hort. Petrop. **6**: 254. 1879.

Slender shrub 1–5 m. high, branches drooping, often dependent, ribbed, older bark reddish-brown to dark gray, exfoliating, young twigs angled, gray-brown to tan, with a short, dense pubescence, often villous, internodes about half the length of the leaf, leaves in dense fascicles; leaf-blades oblanceolate to obovate, narrow cuneate at the base, decurrent on the petiole, the apex denticulate, rounded to round-obtuse, the lower three-fourths of the blade entire, the upper fourth denticulate, the teeth ending in a sharp, frequently bent mucro, 3–4 on each side, the leaf-blades glabrous to densely white-silky above, white-silky beneath, 1.5–3 cm. long, 0.5–1.5 cm. wide; petioles 1–3 mm. long; inflorescence sparse, spreading, usually narrow, densely villous-pubescent, 5–14 cm. long, 3–10 cm. wide; pedicels 2–3 mm. long, with 3 bracts, these lanceolate to broadly lanceolate, 1–3 mm. long; sepals broadly triangular-ovate with acute apex, 1.5–2 mm. long; petals oval to orbicular with a thick row of short, silky hairs along the back median line, extending to top of petal, more often with scattered pubescence on back, 2–3 mm. long; stamens as long as sepals; carpels villous, 2 mm. long; styles 1 mm. long, achenes often slightly curved on upper surface with a very convex lower surface.

Illustration: Figure 3.

KEY TO VARIETIES

Leaf-blades pubescent above.

Leaf-blades equally white-silky above and beneath.

Sepals with long dense pubescence. Colombia ..... 8a. *H. argenteus* var. *typicus.*

Sepals with short matted pubescence. Chiapas, Mexico ..... 8b. *argentus* var. *Matudai.*

Leaf-blades with a very short pubescence above. Oaxaca, Mexico. 8c. *H. argenteus* var. *velutinus.*

Leaf-blades glabrous to glabrescent above. Chimaltenango (Guatemala) and Costa Rica ..... 8d. *H. argenteus* var. *alpestris.*

8a. H. ARGENTEUS var. **typicus** Ley, var. nov.

Spiraea argentea L. f. Suppl. 261. 1781; *Holodiscus argenteus* Maxim. Acta Hort. Petrop. 6: 254. 1879; *Schizonotus argenteus* Kuntze, Rev. Gen. 1: 225. 1891; *Sericotheca argentea* Rydb., N. Am. Fl. 22: 266. 1908; *Schizonotus argenteus* var. *Mutisianus* O. Kuntze, Rev. Gen. 1: 226. 1891.

Leaf-blades densely white-silky above and beneath; inflorescence 5–11 cm. long, 1–8 cm. wide, the pedicels with narrow lanceolate bracts, these 2–3 mm. long, rarely 1 mm. wide; petals with long, silky hairs along back of median line; sepals extremely villous with many long hairs.

TYPE collected by Mutis in Colombia, given as New Granada. Range, Colombia. *Material seen:* COLOMBIA—SANTANDER: *Killip & Smith 18477, 18179, 17254, 17430, 17310, 18576, 15795* (NY, US). BOYACÁ: *Cuatrecasas 1181, 1299* (US). CUNDINAMARCA: *Pennell 2095* (NY, US), *Cuatrecasas 5416* (US), *Holton 939* (NY), *Triana 4215* (NY, US), *André k 1006* (NY), *Schultze 31* (US), *André k 1007* (NY).

8b. H. ARGENTEUS var. **Matudai** Ley, var. nov.

Laminae foliorum in superficie superiore dense albido-sericeae, inferiore sericeae et villosae; inflorescentia parva, 3.5 cm. longa, 2 cm. lata; pedicellis cum bracteis lanceolatis, usque ad 2 mm. longis; petalis externe pubescentibus, sepalis cum pubescentia breve et densa.

TYPE: Mt. Tacaná, Chiapas, Mexico, *Matuda 2303* (NY; isotypes, MICH). Known only from the type collection.

8c. H. ARGENTEUS var. **velutinus** (Rydb.) Ley, comb. nov.

Sericotheca velutina Rydb. N. Am. Fl. 22: 265, 1908; *Holodiscus velutinus* Standley, Pub. Field Mus. Bot. 4: 210. 1929.

Leaf-blades with a very short, usually dense pubescence above, velvety; inflorescence over 7 cm. long, the pedicels with wide bracts, these broadly

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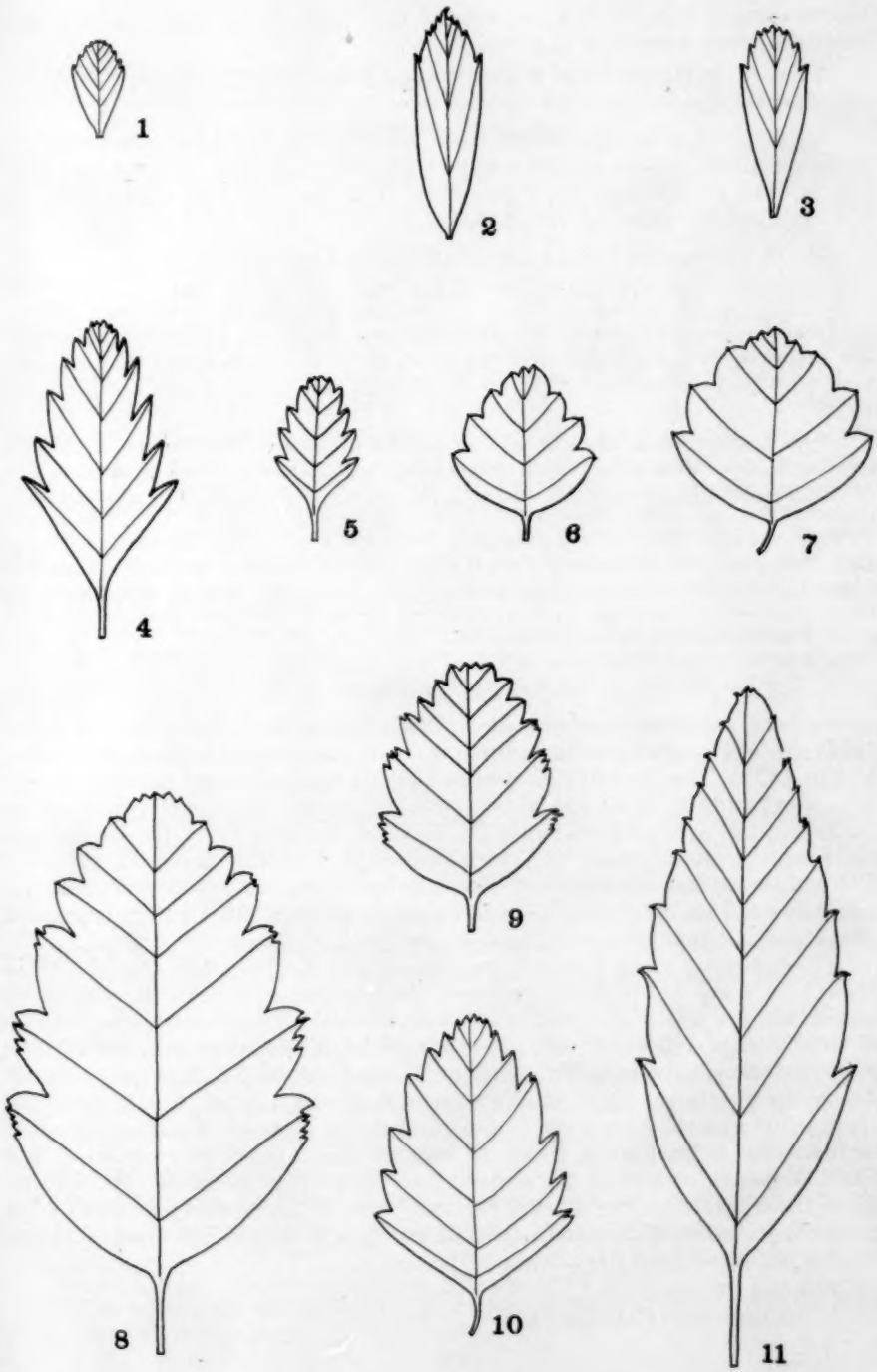
Explanation of figures 1–11

Leaf shapes of the various species of Holodiscus. No shading nor pubescence is indicated. All drawings are made on the same scale; the length given includes blade and petiole. FIG. 1. *H. microphyllus.* Leaf 1.7 cm. long; Duran 3104. FIG. 2. *H. orizabae.* Leaf 2.9 cm. long; Liebmann 1670. FIG. 3. *H. argenteus.* Leaf 2.3 cm. long; Killip and Smith 17254. FIG. 4. *H. dumosus* var. *australis.* Leaf 3.7 cm. long; Wolf 2842. FIG. 5. *H. dumosus* var. *typicus.* Leaf 2.1 cm. long; Osterhout 2121. FIG. 6. *H. Boursieri.* Leaf 2.15 cm. long; Greene 1431. FIG. 7. *H. pachydiscus.* Leaf 2.8 cm. long; Bourgeau 267. FIG. 8. *H. discolor* var *typicus.* Leaf 7.1 cm. long; Thompson 9818. FIG. 9. *H. discolor* var. *franciscanus.* Leaf 4 cm. long; Santa Cruz Mts., San Mateo Co., Bond in 1928 (POM). FIG. 10. *H. discolor* var. *delnortensis.* Leaf 3.2 cm. long; Parks 24019. FIG. 11. *H. fissus.* Leaf 8.4 cm. long; Heyde and Lux 3034.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lanceolate and with acute apex, often 4 mm. long, 1 mm. wide; silky pubescence scattered over back of petal.

TYPE: Sierra de San Felipe, Oaxaca, Mexico, *Smith 821* (NY; isotype, US). Known only from the type locality. *Other material seen:* MEXICO—OAXACA: *Nelson 1085* (US).

Although this variety differs from var. *typicus* in lacking the silky appearance above, it does not seem to be sufficiently distinct to be made a separate species as Rydberg (op. cit.) does. The leaf size and shape, and the inflorescence are very like var. *typicus*.

8d. H. ARGENTEUS var. **alpestris** (Kuntze) Ley, comb. nov.

Schizonotus argenteus var. *alpestris* Kuntze, Rev. Gen. **1**: 226. 1891.

Leaf-blades glabrous above; inflorescence 5–11 cm. long, 3–8 cm. wide, the pedicels with wide, lanceolate bracts, these 2–3 mm. long, up to 1 mm. wide; silky pubescence scattered over back of petal, particularly along veins.

Type locality, Irazú, Costa Rica, 3300 m. Range, Dept. Chimaltenango, Guatemala, and Costa Rica. *Material seen:* GUATEMALA—CHIMALTENANGO: *Standley 61842* (NY), *Skutch 430* (MICH, US), *Skutch 97* (US), *Seler 2364* (NY, POM, US). COSTA RICA—CARTAGO: *Herbarium of O. Kuntze 2358* (NY), *Pittier & Durand 187* (US), *Orsted 1668* (NY, US), *Pittier 14101* (US), *Niederlein* (US), *Stork 345* (US), *Rowlee & Stork 911* (NY, US). SAN JOSÉ: *Standley & Valerio 43555, 43962* (US). One specimen—plains near Teepám, Dept. Chimaltenango, Guatemala, *Skutch 544* (US)—has an acute apex and conspicuous teeth, resembling *H. fissus;* however the small size and villous condition beneath would indicate it to be var. *alpestris*.

UNCERTAIN SPECIES

Spiraea mexicana Schiede, ined. 1835; Regel, Ind. Sem. Hort. Petrop. **1857**: 58. 1858. (*Schizonotus argenteus* var. *mexicanus* Kuntze, Rev. Gen. **1**: 226. 1891). The type of this species was not available, and the description is so short as to be of no aid in determining status. The country is given as unknown, but it would evidently be Mexican. Kuntze (l.c.) places the var. *mexicanus* in his key near to *Schizonotus argenteus* var. *fissus*. He does not cite specimens and consequently it is not known whether this specimen was accessible to him. Schneider (Handb. Laubh. **1**: 497. 1905) in his treatment of the genus cites this species as a synonym of *H. fissus*.

The following varietal names proposed by O. Kuntze, Rev. Gen. **1**: 225–6 (1891), in a key but without sufficient descriptions and without citation of specimens, are uncertain: *Schizonotus argenteus* var. *angustissimus*, may be *H. orizabae; S. argenteus* var. *griseus*, may be *H. dumosus* var. *Schaffneri; S. argenteus* var. *intermedius*, may be *H. pachydiscus*. Mexican and South American specimens were studied from both the United States National Herbarium and the New York Botanical Garden. None of this material could be identified as that upon which O. Kuntze based the above varieties. The Field Museum contained no material of *Holodiscus* collected by Kuntze. Since these three institutions are the only ones in this country known by me to have specimens of Kuntze's, it has been impossible to determine in which species Kuntze's varieties should be placed.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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THE SECTION SEDASTRUM OF SEDUM[1]

ROBERT T. CLAUSEN

Sedastrum was first described as a genus by Rose in 1905 (N. Am. Flora **22**(1): 58). As basis for the generic status distinct from *Sedum,* Rose cited the dense basal rosettes of leaves, the numerous stems dying down to the base after flowering, the more or less paniculate inflorescences and the erect carpels concave under the scales. Berger (in Engl. & Prantl, Nat. Pfl. ed. 2. **18a**: 445. 1930) reduced the genus to the status of a section of *Sedum,* mentioning as characteristics the details already indicated by Rose, also the more or less fleshy, thickened rootstocks. Fröderström[2] designated *Sedastrum* as Group 10 of his Section *Americana Orthocarpia.* As diagnostic characteristics, he mentioned the usually pubescent, dense, *Sempervivum*-like basal rosettes, the paniculate inflorescences and the very thin, usually wavy petals.

The floral structure of *Sedastrum* seems sufficiently similar to the condition in *Sedum* to justify the continuance of this group of species in subgeneric rank rather than as a full genus. The vegetative characteristics which seem most important are the dense rosettes of leaves at the bases of the stems, the habit of the fertile shoots dying back to the base after flowering, and the thick rootstocks. The concavity of the carpels behind the scales, originally pointed out by Rose, perhaps is also important. As now understood, there are six species, all of which occur in Mexico, ranging from southern Coahuila to central Oaxaca.

The characters available for separating species of *Sedastrum* are mostly afforded by the vegetative structures—the habit of the plants, shape of leaves and pubescence. The flowers seem to be rather similar throughout the section, although the inflorescences vary considerably. The interpretation presented here is based largely on the examination of herbarium specimens, supplemented by study and observation of fresh plants, in cultivation, of four of the species. The present paper is not a final pronouncement on *Sedastrum,* but merely presents a summary of some of the available information and explains various names which I have used in identifying specimens. Before a final account of this section is possible, much more collecting and observation must be done in Mexico and careful cytological and genetical studies must be made.

The center of distribution for *Sedastrum* seems to be central Mexico, the area in which the largest number of species occurs. Differentiation seems to

[1] Studies in the Crassulaceae—IV.

[2] **Fröderström, Harold.** 1935. Group 10. *Sedastrum. In:* The genus *Sedum,* Part IV. Acta Hort. Got. **10**(Appendix): 72–79. *pl. 45–52.*

have developed from this center, but available data are insufficient at present to warrant speculation on the topic of phylogeny within the section.

In the following account, names of herbaria are abbreviated as: BH, Bailey Hortorium, Cornell University; CU, Department of Botany, Cornell University; NY, New York Botanical Garden; Pom, Pomona College; and US, United States National Herbarium.

KEY TO THE SPECIES OF SECTION SEDASTRUM

A. Flowering stems erect (sometimes short decumbent); plants glabrous or hairy ..... B
  B. Plants glabrous or hairy, but never densely pubescent.
    C. Leaves oblong, ovate or cordate ..... D
      D. Plants large, ranging in height from 30–58 cm.; branches of inflorescence 2–30 cm. long ..... 1. *S. ebracteatum*
      DD. Plants smaller, ranging in height from 15–30 cm. ..... E
        E. Leaves thick, glabrous; carpels glandular ..... 2. *S. glabrum*
        EE. Leaves thin, somewhat hairy; carpels smooth ..... 3. *S. chapalense*
    CC. Leaves narrowly linear or oblanceolate ..... 6. *S. Hemsleyanum*
  BB. Plants densely pubescent ..... 4. *S. Hintonii*
AA. Flowering stems procumbent or prostrate (sometimes hanging) ..... 5. *S. incertum*

1. SEDUM EBRACTEATUM A.P. DC. in Mém. sur la Fam. des Crassulacées, 37. *pl. 6, fig. B.* 1828. In the original diagnosis, the stem was described as tortuous and creeping at the base, with the flower-bearing part erect and the leaves glabrous. The figure shows a completely glabrous plant with thick fleshy oblong or ovate blunt leaves and with a much branched, paniculate cyme. A definite type locality was not designated. Both description and figure were obtained from Mocino's unpublished *Flore du Mexique*. Saunders (Ref. Bot. **4**: *pl. 221.* 1871) published a colored plate of this species with the basal leaves obovate, pale green and glabrous; and the stems glabrous. No pubescence appears in the colored plate except that the sepals seem to be ciliate. Hemsley (Diag. Pl. Nov. **1**: 11. 1878) redefined the species, apparently basing his conclusions on a cultivated plant in the herbarium at Kew. He stated that the species was poorly described by Saunders, but Saunders' description seems to check reasonably well with that of De Candolle. Hemsley described the leaves as oblong and white-pubescent and the cymes as spreading, also he wrote that the flowering branches are erect. Probably Hemsley had a specimen of a pubescent phase of the species, not an exact match for the plant illustrated by De Candolle.

Sedastrum ebracteatum (DC.) Rose, N. Am. Fl. **22**: 59. 1905.

Sedastrum rubricaule Rose, N. Am. Fl. **22**: 59. 1905. Based on plants collected by Dr. E. Palmer near Concepcion del Oro, State of Zacatecas, Mexico, Nov. 22, 1902 (*No. 386*). I have seen specimens from this collection. They are similar to the specimen figured by De Candolle. Like the type of the species they are almost glabrous and not to be regarded as varietally distinct on this basis.

Sedum rubricaule (Rose) Praeger, Jour. Roy. Hort. Soc. **46**: 132. 1921.

Sedum barrancae M. E. Jones, Contr. West. Bot. **18**: 37. 1935. I have seen the TYPE, which is *No. 191717* in the herbarium of Pomona College. It is the collection of M. E. Jones, *No. 27845*, Nov. 17, 1935, from wet loose soil

under cliffs at La Barranca, Guadaljara, Mexico. Jones did not mention how to distinguish his species *S. barrancae* from *S. ebracteatum, S. incertum* or any other species of *Sedum*.

Sedum ebracteatum var. *rubricaule* (Rose) Fröderström, Act. Hort. Bot. **10**(Append.): 73. 1935.

Tufted perennial with stems rigidly erect or short decumbent, 30–58 cm. high, glabrous or puberulent towards bases; rootstock fleshy-thickened, with fibrous roots and one or several dense rosettes of fleshy yellow-green leaves, obovate to ovate-elliptical, and either hairy or smooth; flowering stems green speckled with purple upwards, 8–10 mm. thick at base, 4–7 mm. thick just below inflorescence; cauline leaves oblong, oblong-lanceolate, elliptical or ovoid, blunt or acute, often clasping at base, 0.5–3.8 cm. long, 0.5–1.0 cm. wide, mostly reflexed and withered at time of flowering; inflorescence a lax, spreading paniculate cyme, with the branches 2–30 cm. long; flowers sessile, 5-merous; sepals green, oblong-ovate, obtuse, 2–3 mm. long, unequal; petals white with green median stripe dorsally, spreading or recurved, broadly oblong-ovate, 5–6 mm. long, united below; stamens 3–4 mm. long with filaments white and anthers pink; scales nearly square, about 1 mm.; carpels greenish, 4–6 mm. long, connate at base, with styles divaricate.

S. ebracteatum occurs under and about cliffs in central Mexico in the States of Hidalgo, Jalisco, Zacatecas and Durango. Specific altitudinal data are not available.

Specimens seen: northernmost—Concepcion del Oro, State of Zacatecas, *Edw. Palmer 386* (NY); easternmost—near Dublan, State of Hidalgo, *J. N. Rose & Robert Hay 218* (NY); westernmost—Guadalajara, State of Jalisco, *M. E. Jones 27845* (Pom); southernmost—same as westernmost; oldest—Nov. 22, 1902, Concepcion del Oro, *Edw. Palmer 386*. Number of collections seen—6.

Flowering time seems to be November.

Principal variations are in pubescence and habit. Some plants are glabrous, others are very pubescent. Likewise, the flowering stems may be erect from the base or procumbent.

S. ebracteatum is occasionally cultivated in greenhouses in temperate regions. Plants from cultivated sources have been correctly named.

2. SEDUM GLABRUM (Rose) Praeger, Jour. Roy Hort. Soc. **46**: 127. 1921.

Sedastrum glabrum Rose, N. Am. Flora **22**: 59. Based on plants collected by Dr. E. Palmer at Saltillo in the State of Coahuila.

Perennial with stems erect or very short decumbent, 15–30 cm. high, usually glabrous throughout; rootstocks fleshy thickened, bearing one or several thick rosettes of fleshy, yellow-green, oblong, acute leaves which are convex dorsally, flat on the ventral face, 0.5–4 cm. long, 0.2–1.8 cm. wide and 0.2–0.7 cm. thick; flowering stem 2–6 mm. in diam. at base, 0.5–4 mm. in diam. just below inflorescence; cauline leaves oblong, acute, crowded, somewhat ascending at time of flowering, 0.2–2.7 cm. long, 0.1–0.9 cm. wide; inflorescence a paniculate cyme with the branches either ascending or recurved, 0.5–11 cm. long; floral bracts similar to the leaves, but markedly reduced upwards; flowers sessile or almost so; sepals green, oblong-ovate, obtuse, 2–3

mm. long; petals white, spreading, oblong-lanceolate, acute, 6 mm. long; stamens 4 mm. long; scales almost square, less than 1 mm., carpels greenish, 5 mm. long, glandular.

Known to me only from limestone hills near Saltillo, Coahuila (*E. Palmer 732* and other collections [NY]; and *C. G. Pringle 10090* [CU]), at an elevation of about 1830 m.; and from Santa María del Río, San Luis Potosí, *E. Palmer* (NY). The rosettes of the plants from San Luis Potosí are somewhat hairy. Number of collections seen—5.

The period of flowering seems to extend from July to September.

Sedum glabrum is rarely cultivated. From the horticultural trade I have received it as *Sedastrum Palmeri* (a manuscript name of Rose, used on herbarium labels and published in synonymy by Fröderström, Acta Hort. Göt. **10**(Appendix): 78. 1935). Plants cultivated at the New York Botanical Garden under another of Rose's manuscript names, *S. turgidum* (also published in synonymy by Fröderström, l.c.) are doubtfully to be referred here.

3. SEDUM CHAPALENSE S. Watson, Proc. Am. Acad. **22**: 411. 1887. Based on a specimen from Chapala, State of Jalisco, Mexico, collected by Dr. E. Palmer and preserved at the Gray Herbarium.

Sedastrum chapalense Rose, N. Am. Flora **22**: 59. 1905.

Perennial from a stout rootstock bearing one or several dense rosettes of obovate or ovate, acute, puberulent leaves; flowering stems 10–20 cm. high, glabrous, with the leaves ovate, acutish, 0.4–2.0 cm. long, puberulent; inflorescence a paniculate cyme with the branches more or less recurved and the sessile flowers densely crowded; sepals oblong-ovate, acutish, 2–3 mm. long, green; petals broadly oblong-ovate, acute, contracted towards the base, 5 mm. long, white; stamens 3–4 mm. long; nectar scales rounded at apex, broadest at base, about 0.5 mm. wide and 0.5 mm. long; pistils 5 mm. long, greenish, smooth.

Known at present only from the region of the type locality, Chapala, in the State of Jalisco, at an altitude of 1700 m. This species apparently is not cultivated.

When more collections are available, they may prove that *S. ebracteatum, S. glabrum* and *S. chapalense* are conspecific. Not enough material is now at hand to warrant such lumping, but the differences between these several so-called species seem relatively unimportant.

4. **Sedum Hintonii** Clausen, sp. nov. Figure 1. *Sedum*, sectionis *Sedastrum*, dense pubescens; rhizoma robusta prostrata, 5 mm. diam., rosulas densas ferens; folia rosularum congesta, anguste oblonga vel elliptica, 1.5–5 cm. longa et 0.3–1.0 cm. lata, apice obtuso, fulva quando sicca; caules floriferi ad 24 cm. alti, foliis lanceolatis, acutis, amplexicaulibus, 10–12 mm. longis, 4–5 mm. latis; inflorescentia cyma paniculata, ad 15 cm. longa, ramis late divaricatis; flores sessiles; sepalae 5, ellipticae-ovatae, obtusae, 2.5 mm. longae, 1.2 mm. latae; petalae 5, oblongae-lanceolatae, patentes, 4–5 mm. longae, 1.5 mm. latae; stamina 10, 2–4 mm. longa; squamae oblongae (fere quadratae), 0.3 mm. longae; carpella 5, 4 mm. longa; interius gibbosa, breviter connata ad basim, stylis gracilibus; semina rubra, subpyriforma, 0.7 mm. longa.

Perennial herb with prostrate stout rootstock, 5 mm. in diam., bearing slender roots and several dense rosettes; stems, leaves, branches of the inflorescence and sepals all densely pubescent with the hairs white, hyaline, mottled and somewhat flattened and stiff, to 1.5 mm. long; leaves of the rosettes crowded, narrowly oblong or elliptical, 1.5–5 cm. long, 0.3–1.0 cm. wide, obtuse at apex, yellowish brown when dried; flowering stems to 24 cm. high with the leaves lanceolate, acute, cordate clasping at base, 10–12 mm. long, 4–5 mm. wide; inflorescence a paniculate cyme to 15 cm. long with the branches widely spreading and the flowers crowded, and sessile, 3–10 on a branch; sepals 5, elliptical-ovate, obtuse, 2–2.5 mm. long, 1.2 mm. wide; petals 5, oblong-lanceolate, spreading, with crisped margins, 4–5 mm., 1.5 mm. wide; stamens 2–3 mm. long; nectar scales oblong (almost square), 0.3 mm. long; carpels 5, 4 mm. long, ventrally gibbous, briefly connate at base, with the styles slender; seeds red, subpyriform, 0.7 mm. long. Pinzan, 830 m., Coalcoman, State of Michoacan, April 13, 1941, *G. B. Hinton et al. 15926* (TYPE US *1808082*).

This species, known at present only from the type collection, differs from the other described Sedastrums in the abundant and peculiar pubescence, the flowers densely crowded on the branches of the inflorescence and the small lanceolate cauline leaves. It is probably nearest to *S. chapalense* and may be derived from that species. I am grateful to Mr. C. V. Morton, of the United States National Herbarium, for bringing to my attention Hinton's collection of the new species.

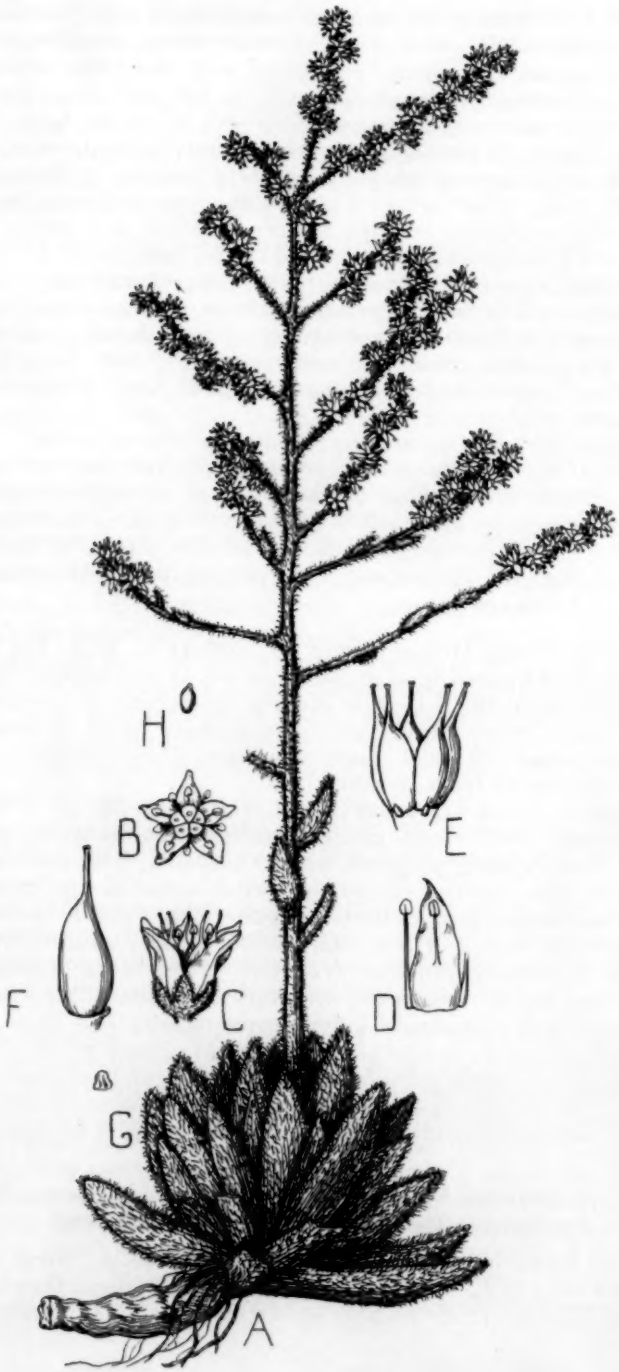
5. SEDUM INCERTUM Hemsley Diag. Pl. Nov. **1**: 11. 1878. The type in the herbarium at Kew has not been available to me. It is the collection of Bourgeau, *No. 1181*, from the Valley of Mexico. The original description seems reasonably clear: leaves fleshy, glabrous, broadly ovate or almost round, obtuse; flowers sessile in short congested cymes. This description fits rather well various specimens from Mexico.

Sedastrum incertum (Hemsley) Rose, N. Am. Fl. **22**: 59. 1905.

Lax perennial with stems procumbent or even hanging, glabrous or puberulent towards base; rootstock fleshy thickened, with fibrous roots and one or several dense rosettes of lustrous yellow-green fleshy leaves, ovate to oblong-elliptical and either glabrous or puberulent; stems 15–38 cm. high, 3–8 mm. thick at base, 1–3 mm. thick towards top; cauline leaves ovate, oblong-ovate, broadly elliptical or orbicular, blunt, often broadly rounded, 0.5–3.0 cm. long, 0.4–1.7 mm. wide; inflorescence a paniculate cyme with the individual branches of a single inflorescence usually less than 4 cm. long and bearing 1–6 flowers; flowers sessile, 5-merous; sepals green, oblong-ovate, obtuse, 2 mm. long; petals white, often with green median stripe, spreading or recurved, broadly oblong-ovate, 4–5 mm. long; stamens 5 mm. long with red anthers; scales subquadrate, about 1 mm.; carpels greenish, 4–5 mm. long.

S. incertum occurs on ledges and cliffs in central Mexico in the State of Hidalgo and the Federal District, probably also elsewhere.

Specimens seen:—northernmost—near Tula, 2068 m., State of Hidalgo, *C. G. Pringle 8693* (CU, NY); southernmost—cliffs above Guadalupe, Federal District, 2286 m., *C. G. Pringle 8693 1/2* (CU, NY). Number of collections seen—6.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Flowering time seems to be October and November. Cultivated plants, received as *S. incertum* and *S. ebracteatum,* flowered at Ithaca, N. Y., in December and January.

6. SEDUM HEMSLEYANUM Rose, Bull. N. Y. Bot. Gard. **3**: 41. 1903. Based on three Mexican collections: *F. Muller 322* from Orizaba, *C. G. Pringle 6042* (TYPE) from near Oaxaca City, and *E. W. Nelson 2001* from between Petlacingo and Acatlan. I have examined representatives of all three collections.

Sedastrum Hemsleyanum Rose, N. Am. Fl. **22**: 58. 1905.

Sedastrum Painteri Rose, N. Am. Fl. **22**: 58. 1905. Based on plants collected near Cuernavaca, Mexico, and differing from *S. Hemsleyanum* primarily in being less pubescent and having oblanceolate cauline leaves. Specimens of the type collection impress me as being very similar to *S. Hemsleyanum* and not specifically distinct.

Sedastrum pachucense C. H. Thompson, in Trans. St. Louis Acad. **20**: 21. *pl. 10.* 1911. Based on plants collected at Pachuca in August, 1910. The illustrations accompanying the original description, depicting this species and *S. Hemsleyanum,* demonstrate the great similarity between the two. Praeger[3] has indicated the differences between them, but these impress me as relatively unimportant and not reliable.

Sedum pachucense Praeger, Jour. Roy. Hort. Soc. **46**: 128. 1921.

Sedum Painteri A. Berger, in Engl. & Prantl, Nat. Pfl. ed. 2. **18a**: 445. 1930.

Tufted perennial with stems erect or spreading, 10–26 cm. long, glabrous or pubescent; rootstock somewhat thickened, with several dense rosettes of spatulate, elliptical, or oblanceolate leaves, 0.5–1.0 cm. long, 0.1–0.3 cm. wide, blunt; cauline leaves, linear, narrowly elliptical or oblanceolate, usually terete or almost so, green or red, 3–20 mm. long, 0.5–4.5 mm. wide, acute or obtuse; inflorescence a paniculate cyme, 4–9 cm. long, with the branches 0.7–2.5 cm. long; sepals ovate-elliptical, acute or obtuse, 1.5–3 mm. long; petals white, oblong-lanceolate, 3–4 mm. long; stamens 2 mm. long; scales subquadrate, yellowish; carpels 4–5 mm. long, greenish white, with the styles slender to divergent.

S. Hemsleyanum grows on ledges and rocky banks at elevations of 1250–1700 mm. in the States of Hidalgo, Morelos, Oaxaca, Puebla and Vera Cruz.

Specimens seen:—highest altitude—1700 m., vicinity of Cuernavaca, State of Morelos, Dec. 1, 1932, *H. Fröderström & E. Hultén 536* (NY); lowest altitude—1250–1463 m., between Petlacingo and Acatlan, State of

Explanation of figure 1

FIG. 1. *Sedum Hintonii.* Drawings by Miss Julia Donaldson from the type collection. A. Habit sketch (×0.7). B. Flower from above (×2.25). C. Flower from side (×2.25). D. Petal and two stamens (×3.5). E. Carpels (×3.5). F. Single carpel (×4.5). G. Nectar scale (×7). H. Seeds (×7).

[3] **Praeger, R. L.** 1921. An account of the genus *Sedum* as found in cultivation. Jour. Roy. Hort. Soc. **46**: 1–314.

Puebla, Nov. 20, 1894, *E. W. Nelson 2001* (NY); northernmost—Pachuca, Hidalgo, the specimens described as *Sedastrum pachucense;* easternmost—Orizaba, Aug., 1853, *F. Müller* (NY); westernmost—same as lowest altitude; southernmost—near Oaxaca, State of Oaxaca, Nov. 12, 1894, *C. G. Pringle 6042* (NY); oldest—1853, Orizaba, *F. Müller.* Number of collections seen—12.

Flowering time, as determined from data with herbarium specimens, extends from September to December. Plants in cultivation in eastern United States usually flower in December and January.

S. Hemsleyanum differs in the degree of pubescence, the amount of red pigmentation and the relative acuteness or bluntness of the cauline leaves. Not enough specimens are yet available to demonstrate the degree of significance of these variations.

SUMMARY

Sedastrum is maintained as a section of *Sedum.* Six species are recognized, one of which, *S. Hintonii* from the State of Michoacan, is described as new. Four species, previously described, are relegated to synonymy.

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A PRELIMINARY INVESTIGATION OF THE NORTH AMERICAN CANES (ARUNDINARIA)

CHARLES L. GILLY

During the course of certain recent routine identifications, the problem of specific delimitation within the native canes of North America was again brought to my attention.[1] When the specimens in question were determined by means of the available keys to the genus there seemed to be scant question of their identity, for the differences given between *Arundinaria tecta* and *A. gigantea* (*A. macrosperma*)[2] seemed adequate for differentiation between the two species therein recognized. However, a subsequent comparison with material in the herbarium raised the question whether the differences given in the keys were really fundamental. From the preliminary examination of the available material it seemed that it would be advisable to make a further study in an attempt to ascertain if there might be differences, other than those of growth-habit, which could be used to separate unit-entities within the North American *Arundinaria* population.

A review of the literature on the native canes revealed that Brown has questioned the advisability of using the habital differences for specific delimitation.[3] Upon the basis of a study of material from Louisiana, he decided that only one species was present in that state; that it exhibited, under various conditions of growth, the two habital forms considered as typical of the two species (or species and variety) usually recognized. My study of the specimens available in the herbarium of the New York Botanical Garden supports Brown's contention so far as the Mississippi Valley and certain adjacent regions are concerned. However, an examination of specimens from the Atlantic Coastal Plain of Virginia and North Carolina leads me to believe that Brown was not justified in further assuming, on the basis of material from only one portion of the total distributional range, that all populations of *Arundinaria* in North America are to be included in a single species. It should be noted that Brown, like most others who have worked with North American *Arundinaria*, apparently did not consider the structural charac-

[1] "North America" as used throughout this paper excludes Mexico; the species of *Arundinaria* in that country and throughout Central America do not appear to be directly concerned in the present problem.

[2] The names *A. tecta* (Walt.) Muhl. and *A. gigantea* (Walt.) Chapm. are used for the two species recognized by Hitchcock (**Hitchcock, A. S.** 1935. Manual of the grasses of the United States, 29–30, 802–803). *A. macrosperma* Michx. is usually regarded as synonymous with *A. gigantea*, and is used instead of the latter name for the "large cane" of several of the current manuals.

[3] **Brown, C. A.** 1929. Notes on *Arundinaria*. Bull. Torrey Club **56**: 315–318.

ters of the spikelets; at least he makes no mention of these organs, other than to specify the manner of their arrangement in inflorescences.

A consideration of descriptions and keys in the currently available manual treatments of *Arundinaria*,[4] and of the original descriptions of the various specific or subspecific entities proposed in the North American segment of the genus, reveals one very surprising thing. Although the morphological characters of spikelets and florets are considered as providing the fundamental diagnostic characters for the classification of the grasses, these characters have almost never been utilized in studies of the native North American canes. Britton (l. c.) and Britton and Brown (l. c.) published the only American manual treatments in which the spikelets have been considered much beyond the fact that they are sometimes present on the plants. Even here the spikelets were given no real emphasis, and were not used in the differentiation of the species recognized by these authors. Ruprecht and Munro, European students of the Bambuseae, considered the characters of the spikelets in some detail.[5] The former utilized spikelet differences to separate varieties of *A. tecta*, and the latter mentioned certain of these differences but rejected them on the basis of apparent "intermediates" available to him.

It is pertinent to this discussion to note that the specimens from which the illustrations of *A. gigantea* and *A. tecta* in Hitchcock's Manual (l. c., figs. 1 and 2) were drawn both came from Virginia (*Chase 5880* and *5881*). Although I have not seen these particular specimens, the illustration of *A. tecta* agrees exceedingly well with a specimen collected in Virginia by Mrs. Chase, and widely distributed as *Amer. Gr. Nat. Herb. no. 498*. The dimensions of the spikelets as illustrated for *A. gigantea* indicate that they are quite similar to those illustrated for *A. tecta*. When the spikelets of the Chase specimen from Virginia were compared with those of *Brown 4048* (the only specimen from Louisiana available to me), certain rather striking differences, which appeared to merit further consideration, were observed.

[4] **Britton, N. L.** 1901. Manual of the flora of the Northern States and Canada, 185. In subsequent editions the treatment of *Arundinaria* is unchanged. **Britton, N. L., & Brown, A.** 1913. An illustrated flora of the Northern United States, Canada and the British Possessions. ed. 2. **1**: 295. **Hitchcock, A. S.** 1935. Manual of the grasses of the United States, 29, 30. **Robinson, B. L. & Fernald, M. L.** 1908. A handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada [Grays' New Manual of Botany, Edition 7], 1–171. **Small, J. K.** 1933. Manual of the Southeastern Flora, 138, 139.

[5] **Ruprecht, F. J.** 1839. Bambuseae. [separate from] Act. Acad. Caes. Petrop. VI. **5**(2): 1–74. *pl. 1–18*. This was reprinted with different pagination early in the following year; the correct citation of this second issue, according to data published by P. L. Ricker (Proc. Biol. Soc. Wash. **21**: 11–18. 1901.), is as follows: Mem. Acad. St. Petersb. **5**(2; Sc. Nat. **3**): 91–165. *pl. 1–18*. 1840. Hitchcock (l. c.) has used essentially this last citation in the listing of certain Ruprecht names, but has erroneously given the date as of the earlier extract. **Munro, Col. W.** 1868. A monograph of the Bambuseae, including descriptions of all species. Trans. Linn. Soc. **26**: 1–157.

The next step in this preliminary study was to sort all available spikelet-bearing specimens of North American *Arundinaria* into two groups, using the spikelet characters of the Chase and the Brown specimens as criteria for this sorting. Most of the specimens examined could easily be referred to one or the other of the two groups, but a few were apparently intermediate in varying degrees; these "intermediates" will be more fully discussed in a later paragraph. It was discovered, when the sorting of specimens had been completed, that those with spikelets similar to those of the Chase specimen were almost entirely restricted in distribution to the Atlantic Coastal Plain (see map, fig. 1). For subsequent discussion these will be considered as constituting the *atlantic-type* of North American *Arundinaria*. The specimens with spikelets similar to those of the Brown specimen—although they collectively occupy a much wider distributional area than the name would imply—will be referred to as the *mississippi-type*, because this appears to be the only sort of spikelet represented in the cane populations of the Mississippi Valley.[6] These two spikelet types may be characterized as follows:

Mississippi-type: Spikelets 5–8(–10)-flowered, 3.5–5(–7) cm. long; lemmas green or greenish, densely pubescent or rarely glabrescent in age, with conspicuous transverse thickenings between the nerves, the lower and median lemmas 1.5–2.75 cm. long, tapering to an acuminate, long-acuminate, or subaristate apex; inner glume one-half or slightly less than one-half the length of the lemmas, greenish, pubescent, acute at the apex, the median one of the several equally prominent nerves reaching the apex; outer glume similar to the inner but smaller (figure 2, M1–M4; localities where specimens with this sort of spikelets have been collected are indicated on map, fig. 1, as black disks).

Atlantic-type: Spikelets 5–10(–12)-flowered, 2–4 cm. long; lemmas purple or purplish-tinged, glabrous except for minute marginal ciliation toward the apex, transverse thickenings not visible between the nerves, the lower and median lemmas 0.8–1.5 cm. long, their apices merely acute or somewhat rounded; inner glume never more than one-third the length of the lemmas, purple or purplish, glabrous except for sparse ciliation at the blunt or truncate and generally erose apex, the mid-nerve rarely reaching the apex and the lateral nerves obscure or obsolete; outer glume similar to the inner but much smaller or sometimes lacking (fig. 2, A1–A4; localities where specimens with this sort of spikelets have been collected are indicated on map, figure 1, as black triangles).

From this preliminary study there also appears to be a correlation between type of spikelet and type of leaf sheath in the specimens which I have examined where both spikelets and foliage were present. The type of leaf

[6] Extensive field studies of the North American cane population may perhaps necessitate a future modification of this statement; on the basis of the specimens available to me, there is no evidence of the presence of the *atlantic-type* west of Biloxi, Mississippi, from which locality I have seen an apparently "intermediate" specimen which can be considered as *atlantioid* in spikelet-type.

sheath (fig. 2, M5), which appears to be correlated with *mississippi-type* spikelets, has a densely and conspicuously pubescent exterior-ligule, and the clusters of auricular bristles at either side of the apex of the sheath are more or less united at the base into a triangular wedge of tissue distinctly different in color and texture from the sheath region immediately below. The individual bristles are larger in diameter and more coarsely scabrous than in the *atlantic-type* sheath. In this latter type of sheath (fig. 2, A5) the groups of bristles are not basally united above the apex of the leaf sheath,

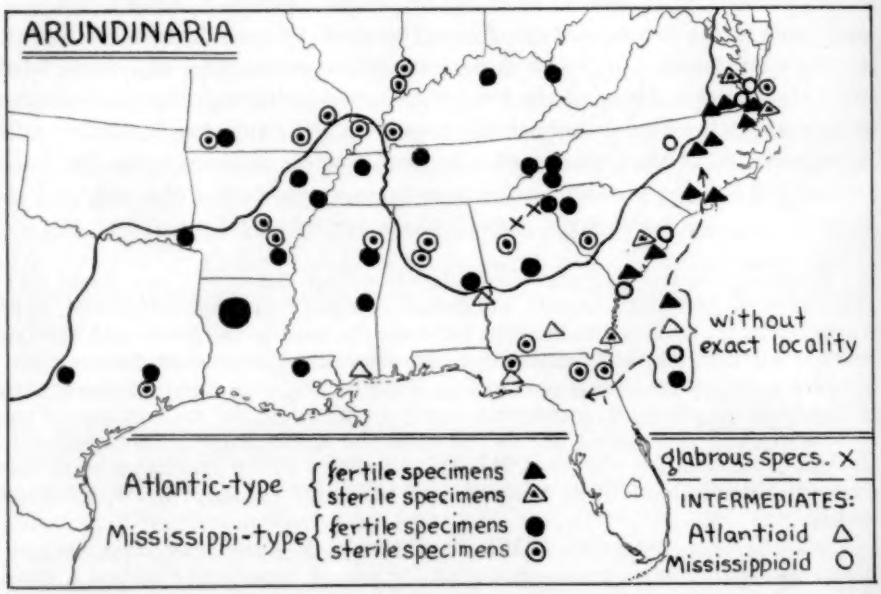

FIG. 1. Distribution of *Arundinaria*, based on specimens in the herbarium of the New York Botanical Garden. The inner boundary of the Coastal Plain is approximately indicated by a heavy line. Some of the symbols on the map represent more than one collection from the same or closely adjacent localities. Illustrations of the spikelet and leaf sheath characters which form the basis of the two types recognized within the genus are presented in figure 2. The localities of two collections, mentioned in the text as being vegetatively glabrous and having somewhat different leaf sheath characters, are indicated by the symbol ×.

and the exterior-ligule is either glabrous or microscopically ciliate. The interior-ligules of both types are variable, although the *mississippi-type* appears to be always more or less pubescent while the *atlantic-type* is either glabrous or sparsely ciliate with bristle-like hairs. The overlapping margin of the sheath proper is either glabrous or minutely pubescent in the *atlantic-type*, while in the *mississippi-type* it is usually coarsely ciliate.

It is perhaps of more than casual interest to note that in the available specimens of South American and Central American *Arundinaria* and *Arthrostylidium* (a closely-related and perhaps not adequately separable

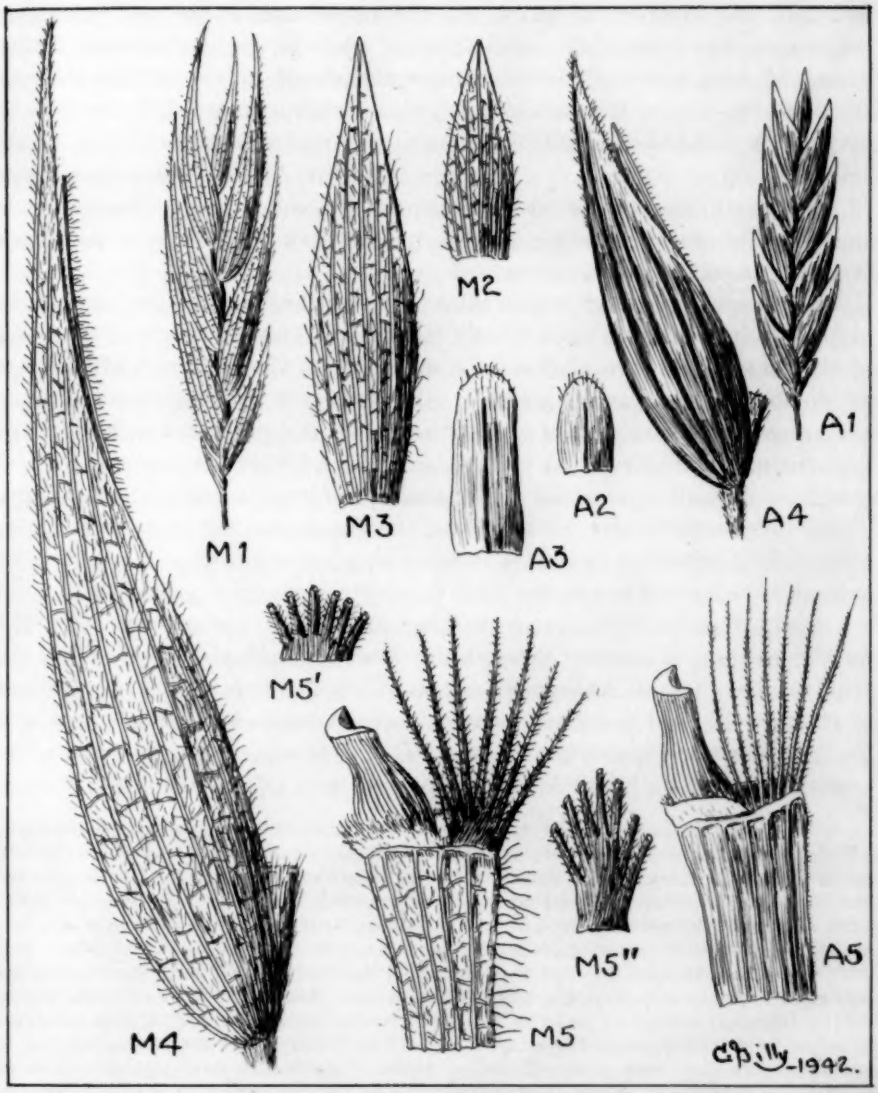

FIG. 2. Morphological characteristics of the two types of *Arundinaria* in North America north of Mexico. A1–A5: the *atlantic-type;* M1–M5: the *mississippi-type.* Portions of the plants illustrated are: 1. spikelets (×1.5); 2. outer glume (×6); 3. inner glume (×6); 4. lemma (×6); 5. apex of leaf sheath (×3). Figures A1–A4 were drawn from *Fernald and Long 6940,* from near Crismond, Nansemond Co., Virginia, and figure A5 from *A. Chase s. n.* (*Amer. Gr. Nat. Herb. no. 500*) from the Back Bay section of Princess Anne Co., Virginia. Figures M1–M4 were drawn from *Bush 198,* from Eagle Rock, Barry Co., Missouri, and figure M5 from *Gattinger s. n.* (*Curtiss' N. Am. Pl. Distrib. no. 3523*) from near Nashville, Tennessee. The range of variability in the degree of basal fusion of the auricular bristles from the *mississippi-type* leaf sheath is indicated in figures M5′ (drawn from *Demaree 13950,* from Jefferson Co., Arkansas) and M5″ (drawn from *Combs 149,* from near Lake City, Columbia Co., Florida); only the basal portion of the cluster of auricular bristles is shown in these last two figures.

genus of the Western Hemisphere) the leaf-sheath apices and auricular bristles are like those of the *atlantic-type*,[7] while in specimens which I have examined from eastern Asia the bristles and sheath-apices are like those of the *mississippi-type*. It seems safe, here, to postulate that this latter type of leaf sheath is characteristic of a Holaretic group of species, the North American segment of which is now disjunct from the Asiatic. The *atlantic-type* of leaf sheath, closely similar in structure to the South American type, is indicative of the relationship of this type of *Arundinaria* with the South American members of the genus.[8]

Specimens apparently intermediate between the *atlantic-type* and *mississippi-type* have already been briefly mentioned. These "intermediates" are of several sorts. In some of them, the characters of the two types of spikelets are combined in varying degrees. In others where both spikelets and foliage are present, some association of *atlantic-type* spikelets with *mississippi-type* leaf sheaths (and vice versa) was evident; also a few of the sterile specimens examined seemed to combine the characters of both types of leaf sheaths. These intermediates are indicated on the accompanying map (fig. 1) by either white triangles or circles, dependent upon the degree in which they seem to approximate one or the other of the two types.

A consideration of the accompanying map (fig. 1) reveals that while the *mississippi-type* is common through the lower Mississippi Valley and on the Gulf Coastal Plain, it is also more or less widely distributed through portions of the two old land masses of eastern North America—the Ozark area and the Appalachian-Cumberland region. The *mississippi-type*, therefore, appears to represent a North American species whose affinities, as already men-

[7] This is particularly apparent in certain as yet unidentified specimens from Honduras (*Yuncker, Dawson & Youse 6085*) and Central Brazil (*Krukoff 7273*) as well as in material identified as *Arundinaria deflexa* E. E. Br. from the summit of Mt. Roraima on the British Guiana–Venezuela–Brazil boundary corner. This latter species, although apparently exhibiting the growth-habit of North American *Arundinaria*, seems to have spikelets approaching those of *Arthrostylidium* in flower number. The sheet of *A. deflexa* (*Tate 471*) in the herbarium of the New York Botanical Garden is sterile, and I know the spikelets of this species only from the original description (**Brown, N. E.** *et al.* 1901. Report on two botanical collections made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. Trans. Linn. Soc. II **6**: 1–109). *Arthrostylidium* appears to represent a further development of several reductionary trends than does *Arundinaria;* these are a decrease in flower number per spikelet, the elimination of sheath bristles in some species, and the acquisition of an herbaceous or a liana habit of growth. Various workers with the Bambuseae have either included *Arthrostylidium* in *Arundinaria*, or have considered it as a closely related genus. Further study of this Caribbean and South American genus may perhaps be essential to the ultimate solution of the problems of the North American *Arundinaria*-complex.

[8] For a discussion of a similar relationship in another plant group, a recent paper in which the North American species of *Gaylussacia* are considered should be consulted (**Camp, W. H.** 1941. Studies in the Ericales: A review of the North American Gaylussacieae; with remarks on the origin and migration of the group. Bull. Torrey Club **68**: 531–551).

tioned are with the species of eastern Asia. Its present much wider distribution is almost certainly due to a migration into the Mississippi-embayment and Coastal Plain as these related areas became available for colonization by plants.[9] The *atlantic-type*, on the other hand, is largely restricted to the Atlantic Coastal Plain although *atlantioid* individuals have been collected in the eastern segment of the Gulf Coastal Plain.

The presence of *mississippioid* individuals on the Atlantic Coastal Plain seems entirely due to a downward and outward migration of this species from the Appalachian upland areas. In the northern-part of the distribution area of the genus this migration would seem to have been along ancient drainage systems.[10] Further south (in South Carolina and Georgia) where *mississippioid* individuals occur, this migration is undoubtedly continuing today. It is to be expected that in at least some of the Atlantic Coastal Plain localities where the *mississippioid* individuals are known, that colonies of the *mississippi-type* may be found; the frequency and extent of these colonies will, in part, depend upon the degree to which this type has been genetically submerged by the *atlantic-type*.

So far as vegetative characters, other than those of the distal portion of the leaf sheath, are concerned, I have been unable to find any correlation with either type of spikelet—except perhaps as regards leaf shape. Leaf size appears to be extremely variable in the series of specimens assigned to both the *atlantic-type* and the *mississippi-type*. Most individuals of the former type, however, seem to have a lanceolate-acuminate leaf blade in contrast to the merely acute and narrowly lanceolate-elliptic leaves present in most individuals of the latter type.

[9] Dr. W. H. Camp informs me that he has seen "cane" growing abundantly in parts of Kentucky and eastern Tennessee, in both states often on hillsides where the forest cover was not too dense. From his description of these areas it is apparent that the habitat is similar to that of various of the *Arundinaria* species in eastern Asia; and, as is well known, these areas of the southeastern United States contain numerous species in other genera and families which have cognate forms in eastern Asia. It is therefore likely that the populations of the *mississippi-type*, so common along the larger streams and rivers, may have been entirely derived from just such hillside populations as those now growing near the heads of the present drainage systems.

[10] Although *Arundinaria* is reported as ranging northward in the interior as far as Highland County, Ohio, and along the coast to New Castle County, Delaware, and Anne Arundel County, Maryland, I have seen no specimens from these localities. It is quite probable that before the Pleistocene the *mississippi-type* had a much more northerly distribution in the Appalachian-Cumberland region. Evidence which seems to support this statement is found in a report of the finding of half-masticated portions of plants of "a species of Arundo, or Arundinaria, still common in Virginia" in the well-preserved stomach of a mastodon (*Mammut americanum*) whose skeleton was discovered in Wythe County, Virginia, in 1806 (**Hay, O. P.** 1914. The Pleistocene mammals of Iowa. Rept. Iowa Geol. Survey **23**(1912); in particular, p. 367 of the section dealing with the food of the mastodon). Rearrangements in the drainage pattern—these, in part, occurring in pre-Pleistocene times—in the region which now includes North Carolina, Virginia, West Virginia, Maryland, and Pennsylvania have perhaps prevented subsequent coast-ward migration of the *mississippi-type* in this area.

Although pubescence of leaf blades and sheaths appears to be variable in individuals of both types, there are a few more or less isolated populations which appear to have always been glabrous; this characteristic is best shown by two collections made by J. K. Small in Georgia, one on the Yellow River in Gwinnett Co. (July 20, 1893), the other in Habersham Co., between Toccoa Falls and Tallulah Falls (Sept. 3, 1894). These particular specimens, both in their glabrous nature and somewhat different leaf sheath characters, are very similar to certain species of *Arundinaria* from eastern Asia. Whether they represent a disjunct remnant of a species or species-complex with a formerly wide Holarctic distribution, or whether these specimens may have been collected from naturalized colonies of one of these East Asian species, can not be decided on the basis of the evidence at present available to me. Further study of the cane populations in these areas will be necessary to clear up this particular point.

Another point, regarding certain Alabama populations of *Arundinaria* described by Harper, also appears to need further investigation.[11] In contrast to Brown's conclusions from a study of Louisiana canebrakes, Harper—after a study of Alabama populations of *Arundinaria*—stated: "This genus is not very fully understood, partly on account of the scarcity of flowers and seeds, and the number of species in North America may be anywhere from one to three or four. In Alabama there seem to be two, or possibly three." Although Harper gave few differences between the species except comparative height, culm diameter and frequency of flowering, he definitely recognized two species as present in Alabama.

A. macrosperma, found "on river banks and in creek swamps, a little below high-water mark," was said to be distributed essentially throughout the state except in the Blue Ridge, Piedmont, and Outer Coastal Plain portions of Alabama. *A. tecta*, which "grows mostly in sandy bogs, wet woods and non-alluvial swamps, south of the coal regions," was listed as occurring in the Blue Ridge and Piedmont areas, and as particularly common through the Outer Coastal Plain. According to Harper this second species had not been found in the northwestern one-fourth of the state. At the end of his discussion of *A. macrosperma* he remarks: "What may be another species, resembling *A. macrosperma* except in size (being smaller) and habitat, grows on sandstone, shale and limestone cliffs in various parts of the state as follows: 1B. On limestone mountain slopes, within a few miles of the Tennessee River in Jackson, Madison and Marshall Counties. 2B. Bluffs near Simpson's Creek, Cullman County. Cliffs near Warrior River, Walker and Tuscaloosa Counties. 3. Near Sylacauga. 11. Hatchetigbee Bluff on Tombig-

[11] **Harper, R. M.** 1928. Economic Botany of Alabama. Part 2. Catalogue of the trees, shrubs and vines of Alabama with their economic properties and local distribution. Geol. Survey Alabama, Monograph 9; in particular, pp. 72–77, *figs. 18–20*.

bee River, Washington County."[12] Although I have examined a number of specimens collected by Harper in Alabama, there are apparently no examples of this upland type of *Arundinaria* in the herbarium of the New York Botanical Garden. The habitat, as given by Harper, is strikingly reminiscent of that of certain Eastern Asiatic species of the genus.

Before briefly discussing the nomenclatural aspect of the problem of the North American canes, it seems necessary to give some consideration to the habital differences which have so long been considered as indicative of specific distinctness. A quotation from Mohr[13] clearly presents these habital differences:

"*Arundinaria tecta* rarely exceeds the height of 12 to 15 feet, and the slender culm branched from the base is seldom half an inch in thickness. Early in spring, apparently every three or four years, the paniculate flowers are produced on naked[14] radical shoots scarcely exceeding 18 inches in height, while the tall flowerless canes are sent up every season from the long creeping rhizomes. *Arundinaria macrosperma*, from 15 to 30 ft. high and frequently an inch and over in diameter, produces the panicles of its flowers in the axils of the branches at long and indefinite intervals of time. . . . The seedlings [of *A. macrosperma*] produce no branches during the first year. These simple shoots, which are known as 'mutton cane' are tender and sweet and afford the best of pasturage."

In regard to the habital characteristics and different modes of flower production, Brown (l. c., pp. 316 and 317) has made the following observations:

"Spikelets of *Arundinaria* were first collected by the writer in March, 1927, in a canebrake near Baton Rouge, Louisiana (*no. 989*). These were from the lower nodes of old canes that had been cut off one or two joints above the ground. In November, 1927, a considerable portion of the canebrake in which the above specimens were collected was cleared. During the last of March and April, 1928, flowers were again found on the lower nodes of the cane stubble. . . . About the first of May there appeared in the same field a large number of somewhat shrubby radical shoots which bore terminal panicles, and according to the manuals should be *A. tecta*. . . . In one of the places where the cane was found in bloom a drainage ditch had been dug in the early part of January, 1928. In this place, flowers were found on both radical shoots and on the old canes. On digging up some of the plants, it was

[12] The numerical designations (1B, 2B, 3, and 11) in the above quotation refer to "natural regions" of Alabama as delimited on map 1, page 33, of Harper's publication.

[13] **Mohr, C.** 1901. Plant Life of Alabama. Contr. U. S. Nat. Herb. **6**. pp. 921. Washington, D. C. Later in the same year this volume was reprinted with identical pagination and issued as a publication of the Geologic Survey of Alabama. The quotation given here is from page 103.

[14] By "naked" Mohr evidently meant the absence of leaves with "blades." The available specimens and illustrations of the "*tectoid*" phase of the cane populations indicate that the culm of the radical shoot is closely covered by overlapping bladeless, or essentially bladeless, sheaths. The specific epithet of Walter's *Arundo tecta*, on which *Arundinaria tecta* is based, is indicative of this character, for it is derived from the latin *tectus*, meaning enclosed or covered.

found that some of the radical shoots with flowers (*A. tecta*) came from the same rootstock as did stalks with lateral spikelets (*A. macrosperma*). . . . A careful examination of several other canebrakes in flower during the spring of 1929 has resulted in finding flowering radical shoots attached to the same rootstock as the old flowering canes. One collection (*no. 2435*) was made near Erwinville, Louisiana, on the edge of a thicket which had not been cut or drained for several years. This suggested that both forms of *Arundinaria* may occur on the same rootstock naturally and that cutting or some other stimulation may not be necessary."

Some of the specimens of the *mississippi-type* which I have examined are clearly from the leafless, sheath-covered radical shoots of the growth-form commonly called *A. tecta*. On the basis of the specimens which I have examined and referred to the *atlantic-type*, it is apparent that tall canes with complexly branched axillary inflorescences and the low radical shoots with terminal inflorescences are both present in this segment of *Arundinaria* as well as in the *mississippi-type* segment. The consecutive collection numbers (*5880* and *5881*) of the Chase specimens from Virginia—previously mentioned as being the basis for the Hitchcock manual illustrations of *A. gigantea* and *A. tecta*—suggests that these two specimens might have been collected from a single Virginia canebrake. If so, they would seem to represent a condition parallel to that observed by Brown in certain Louisiana canebrakes.

Although two distinct types of spikelets are present in the North American *Arundinaria* populations—and these being representative of unit-entities which in all probability are worthy of specific rank—a definite application of names to these entities is not yet possible because the present concepts within the group are based primarily on habital differences.[15] The final solution of the nomenclatural phase of the problem must await (1) a more complete understanding of the variability and complexity of populations within

[15] In future work on the nomenclatural phases of the North American *Arundinaria* problem, it will be necessary to consider (in addition to those already cited in this paper) at least the following publications, all of which have been consulted during the preparation of this preliminary paper: **Camus, E. G.** 1913. Les Bambusées. 1–215. **Chapman, A. W.** 1860. Flora of the Southern United States; in particular, pp. 561 and 562. **Elliott, S.** 1816–1821. A sketch of the botany of South-Carolina and Georgia. Vol. 1; in particular, pp. 96 and 97. **Hitchcock, A. S.** 1905. The identification of Walter's grasses. Rep. Mo. Bot. Gard. **16:** 31–56. 1908. Types of American grasses; A study of the American species of grasses described by Linnaeus, Gronovius, Sloane, Swartz, and Michaux. Contr. U. S. Nat. Herb. **12:** 113–158. 1920. The Genera of Grasses of the United States, with Special Reference to the Economic Species. U. S. Dept. Agric. Bull. **772;** in particular, pp. 22–24. **Michaux, A.** 1803. Flora Boreali-Americana. **1:** 73–74. **Muhlenberg, D. H.** 1817. Descriptio uberior Graminum Plantarum Calamariarum Americæ Septentrionalis Indigenarum et Cicurum; in particular, pp. 191 and 192. **Nuttall, T.** 1818. The genera of North American plants, and a catalogue of the species to the year 1817. **1:** 39. 1837 Collections towards a flora of the Territory of Arkansas. Trans. Am. Phil. Soc. II. **5:** 139–203. **Walter, T.** 1788. Flora Caroliniana; in particular, p. 81.

the genus, and (2) the reexamination of the Walter and Michaux type specimens, now in European herbaria, to determine whether or not the names based on these specimens can be definitely referred to either the *atlantic-type* or the *mississippi-type* of North American *Arundinaria*.

Pending an examination of the existent type specimens, it will be necessary to refer to these two types of *Arundinaria* by names of some sort. It is my suggestion, if the designations *atlantic-type* and *mississippi-type* do not seem to be adequate for this purpose, that the two oldest names seemingly referable on a geographical basis to these two types, be used. The *atlantic-type*, then, could be temporarily referred to as *A. gigantea*, and the *mississippi-type* as *A. macrosperma*. The name *A. tecta*—because no specimen of *Arundo tecta* (on which *Arundinaria tecta* is based) is in the Walter herbarium, and because of the presence of *"tectoid"* phases in both the *atlantic-type* and the *mississippi-type*—should, for the time being, be considered a *nomen dubium*.[16]

In the event that the Walter specimen of *Arundo gigantea* proves to be in such condition that it can not be surely referred to either the *atlantic-* or the *mississippi-type* of *Arundinaria*, I would recommend that the varietal epithet *colorata* of Ruprecht (l. c., p. 22) be raised to specific rank for the *atlantic-type* to which, on the basis of description and accompanying illustration, it is clearly referable. This procedure can, however, be followed only if the type specimen of *A. macrosperma* is definitely determined to be of the *mississippi-type*.[17] Should this specimen prove either to be unidentifiable or of the *atlantic-type*, the only available specific epithet for the *mississippi-type* populations would be Nuttall's *pumila*, for there can be no question as to which type of *Arundinaria* Nuttall was considering when he described *Miegia pumila* (1837, l. c.). However, because of the size connotation, perhaps it would seem to be somewhat unfortunate if it should be necessary to apply this epithet to the predominantly tall canes of the *mississippi-type*.[18]

[16] According to Hitchcock (1905, l. c.) the type of *Arundo gigantea* in the Walter herbarium (in the British Museum) consists merely of a sterile shoot with two leaves; no specimen of *Arundo tecta* is present in the Walter collection. Also, Hitchcock (1908, l. c.) states that the Michaux specimen (in the Muséum d'Histoire Naturelle at Paris) of *Arundinaria macrosperma* is fragmentary and difficult to assign to either of the two species; this last statement is almost certainly made on the basis of habital characters only.

[17] From the wording of the distributional statement accompanying the original description—*"HAB.* ad ripas flum. Mississipi: in Carolina, Florida, &c." (Michaux, l. c.)—it would appear that Michaux collected the type of the species somewhere on the Mississippi River. However, Hitchcock (1908, l. c.) records the data on the label of the type specimen as follows: "Gramen altissimum ramosum a Virginia ad Floridam & in occidentalibus juxta fluviis ad Illinoensibus ad ostium Misissipi." This is suggestive that Michaux's specimen came from somewhere on the Atlantic Coastal Plain.

[18] Actually, the use of this epithet might not be really so unfortunate. If, as is previously intimated in this paper, the lowland populations of the *mississippi-type* have been derived from the upland types now present at the headwaters of certain of the tributaries of the Cumberland-Appalachian drainage systems, then these coarse canes might well be

There perhaps may be some question why I did not borrow and examine all of the specimens of *Arundinaria* available in American herbaria. The problem of the North American native canes has been presented in this preliminary manner for several reasons. In the first place, the need for careful study—over a period of years—of the complex throughout its entire distributional range, the extent of this area of distribution, and the infrequent flowering periods of many populations, makes the problem of delimitation of unit-entities in this segment of *Arundinaria* more than a one-man job. Secondly, it is my belief that the herbarium specimens now on file in our museums are not adequate for the delimitation of entities within the genus. At such time as the biology of the group is more thoroughly understood as the result of detailed and extensive field studies, the specimens at present available—together with those which will be collected in the course of future studies—may be utilized in developing the exact distributional patterns of this segment of the genus.[19] And, lastly, since no definite application of names can be made at the present time—the solution of the nomenclatural phase of the problem outlined in this paper, therefore, being scarcely a prospect of the immediate future—it did not seem advisable at present to examine more material than that available in the herbarium of the New York Botanical Garden.[20]

CONCLUSIONS

In current manual treatments of the North American canes (*Arundinaria*) two species are generally recognized. The differentiation between these species has been made on the relative height of the plants and the manner in which the inflorescence is borne. Since there is evidence in the literature

considered as only a growth-form modification of the upland cane. As Dr. Camp has pointed out in our personal discussion of this matter, the epithet *pumila* certainly would be applicable to much of the upland *mississippi-type* material which, on the basis of available evidence, is conspecific with the *mississippi-type* material of the certainly moister and more fertile lowland habitats.

[19] Despite the irregular flowering periods of certain populations of cane, flowering and fruiting material should be obtained whenever possible. In future collections of sterile material it is suggested that collectors make an attempt to obtain from a single plant specimens from both the current season's growth and the canes of preceding years; it also seems advisable that specimens be taken from at least several plants in a single locality in order to determine the degree of variability in each particular area. Moreover, because of the known variability of the group on the Atlantic Coastal Plain and the eastern segment of the Gulf Coastal Plain, mass collections should be made whenever possible in these regions.

[20] The only exceptions to this statement have been my examination of a fragment of a specimen (*Plymale s. n.*) from the only locality in West Virginia in which *Arundinaria* has been collected, and of fragments of two specimens (*Wells s. n.* and *Buell s. n.*) from North Carolina. These fragments, obtained through the courtesy of Dr. E. L. Core, of the University of West Virginia Botany Dept., and Dr. B. W. Wells, of the North Carolina State College Botany Dept., are now deposited in the herbarium of the New York Botanical Garden.

that a single plant may produce both types of flowering culms, the conclusion has been reached by some workers that only one species is present in North America.

A preliminary examination of species available to me indicates that two types of spikelets, differing in several well-defined characters, are present in the North American cane populations. Since the type specimens necessary to the solution of the nomenclatural phase of this problem are not at present available for study, these two entities have been designated the *atlantic-type* (this one being best developed on the Atlantic Coastal Plain) and the *mississippi-type* (this being the only type apparently present in the drainage basin of the Mississippi River). Since the characters of the spikelets appear to be of fundamental value in the classification of the Gramineae, and since both growth-forms are associated with each of the spikelet types, it seems evident that the habital characteristics used in most former treatments of the group are not to be considered as specifically diagnostic. There is also evidence that certain characters of the leaf sheaths are correlated with the spikelet types. On the basis of these leaf sheath characters, the *atlantic-type* seems to have affinities with the South American members of the group, while the *mississippi-type* seems more closely related to certain of the Asiatic members of the genus.

Despite the fact that intermediates have apparently been produced in certain areas where both the *atlantic-* and the *mississippi-types* occur, it is maintained in this paper that two specific entities are present in the North American populations of *Arundinaria*. These may be distinguished by characters of the spikelets and leaf sheaths, but not by the habital characters generally used in the available treatments of the genus.

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WHAT IS THE TRINOMIAL TYPICUS?—I

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In a recent paper (Rhodora **44**: 157. 1942), Fosberg reveals that a proposal is being circulated to have the Botanical Congress rule out in due course the use of the epithets *typicus, genuinus, verus, veridicus,* and the like. Under this proposal the place of these classic epithets should be taken by the epithet in the binomial. Accordingly, it should be illegitimate or unorthodox to publish *Planta una* var. *typica,* the correct form being solely *P. una* var. *una.*

Such a proposal is not new. One fundamentally like it was advanced by Bolle five years ago (Notizbl. Bot. Gart. Berlin **13**: 524. 1937), and three years ago Fosberg proposed likewise to amend Art. 30 of the current Rules (Am. Jour. Bot. **26**: 229. 1939) which is supposed to be responsible for nomenclatural difficulties when *typicus* and its equivalents are being used.

The recurrent nature of these proposals indicates that the Rules now in vigor leave something to be desired and that changes are necessary. My purpose in writing this article is naturally twofold. I intend to analyze the proposal to which Fosberg alludes and that of Bolle in order to determine whether the measures sponsored therein are pertinent and efficacious. This done, I will briefly state what I believe to be the true nature and function of the trinomial *typicus.* So approached in a spirit of exhaustive discussion the subject at hand will yield not only practical and theoretical considerations but a concrete platform for further competent discussion.

Anyone who intends to modify existing rules, be these rules concerned with the sale of milk in the market of Gopher Junction or with the proper use of taxonomic names in the halls of a botanical institution, should have a clear understanding of three requirements. These requirements are: (1) The proposed amendment must be consistent with the rules that already exist. This means that the amendment must consider what rules say and avoid conflicting with their broader aspects. More definitely: intended changes must be neatly and properly grafted on existing regulations; if conflicts arise between the old and new rules, these conflicts must be smoothed out, either by suitably modifying the proposal itself or by altering the rules that are. Loose ends, contradictions, obscurities are abhorrent to a wise reformer. (2) In no case shall the remedy be worse than the evil which it intends to cure. Heavy drinking is an unmitigated curse but enforced prohibition is just as bad, perhaps worse. A would-be reformer must keep in mind that any rule is bound to be imperfect and carefully weigh the consequences of the changes he sponsors, lest these changes open the door to consequences

even less desirable than the existing inconveniences. (3) The proposed remedies must be applied where they do the most good in the most direct manner. It is useless to deal in generalities and pious wishes without stating the manner of their application to specific cases.

These three principles are not controversial because they speak the voice of common sense. A competent horticulturist does not graft a scion two inches thick on a stock an inch wide; a seamstress does not mend a torn spot in a black dress with coarse white thread; a physician does not leave a potion behind without telling the patient how to take it and when. I restate these principles for reasons that will later be apparent to the reader. Whenever a subject is involved which is controversial and obscure, *it is essential to return to fundamentals*, redefining the major premises of the discussion, informing those who seek the light or need it. To build truly we need solid foundations, readable blue-prints, and precise formulae.

In the copy in my hands, the proposal to which Fosberg alludes reads in part as follows:

"Proposal II. Article 30 a. *Each subspecific group, of whatever rank, which includes the type of the species, shall be designated by the valid specific epithet of the species. For nomenclatural purposes this epithet, when used for a subspecific group, has no authority and no citation and can not be transferred, except as the species to which it is subordinated may be transferred. Each subspecific group which includes the type of the next higher subspecific group but which excludes the type of a species shall be designated by the valid subspecific epithet of the next higher group.*"

This proposal is not likely to appeal to the majority of its readers on the ground that it is worded in highly technical language. This, however, is not in itself a blemish, for it is patent that to deal with technical subjects technical language must be used. It is too much to hope that everything can always be written in colloquial sentences. Obviously, the burden of making technical language understandable, and of understanding it, rests evenly upon the shoulder of the writer and of the reader. If both the parties to the transaction prove incompetent or unwilling, nothing will ever be achieved. It is strange that many who object strenuously against technical language in the Rules of Nomenclature prove to be good bridge players, having at their fingertips a vocabulary staggering to the uninitiated in the game.

The proposal just stated consists of four main parts which must be discussed in detail, as follows:

(1) "*Each subspecific group, of whatever rank, which includes the type of the species, shall be designated by the valid specific epithet of the species. . . .*"

Article 2 of the current Rules of Nomenclature (Amsterdam, 1935) states: "The object of the rules (Art. 19–74) is to put the nomenclature of

the past into order and to provide for that of the future. They are always retroactive: names or forms of nomenclature contrary to a rule (*illegitimate names or forms*) cannot be maintained." This declaration is imperfectly worded, of course, to the extent that it refers to the Articles as "rules," a term which we commonly use in a looser and broader sense. However, it is perfectly clear that, (a) The Articles are always retroactive; (b) Forms and names contrary to an Article cannot be maintained.

This being the case, the proposal advanced by "Art. 30 a" in the clean-cut words quoted above has for its immediate effect to render illegitimate any of the typic trinomials published after 1753 which does not repeat the specific epithet. I believe that this is not the intention of the proponents of "Art. 30 a," but good intentions are meaningless in a world in which only facts count. Either Art. 2 goes as it reads or "Art. 30 a," for there is war between them. My interest in discussing this proposal will be clear to the reader who is told that about one thousand trinomials using *typicus* or *genuinus* instead of the specific epithet repeated are contained in Volume 15 of De Candolle's *Prodromus* (2) which I consult every day. If "Art 30 a" is approved and written into the Rules, all these trinomials are turned into scrap, scrap of a kind which cannot be used otherwise than as synonymy. It stands to reason that "Art. 30 a" runs afoul also of Art. 4 in the current Rules which reads: "The essential points in nomenclature are: (1) to aim at fixity of names; (2) to avoid or to reject the use of forms and names which may cause error or ambiguity or throw science into confusion. Next in importance is the avoidance of all useless creation of names." It is manifest that "Art. 30 a," if approved, will upset the trinomials now in use, throw science into confusion and foster the creation of thousands of new trinomials to replace those which this "Article" would slaughter. Having pointed out these results of "Art. 30 a" in private conversations, I have been told in return that the existing trinomials using *typicus*, *genuinus* and the like should be "quietly ignored." No objection could be raised against their being ignored, quietly or otherwise, if the authors of this "Article" would only state *how* it is possible to elude the precise disposition of Art. 2 and Art. 4. This, "Art. 30 a" does not say, which is a capital omission.

(2) ". . . *For nomenclatural purposes this epithet, when used for a subspecific group has no authority and no citation.* . . ."

The implications of these seventeen words are staggering, for they contain an entirely novel and revolutionary concept of authority and citation, a concept which is unenforceable on account of conflict with rock-bottom realities. Article 15 in the current Rules states: "The purpose of giving a name to a taxonomic group is not to indicate the characters or the history of the group, but to supply a means of referring to it." Article 46 in the same Rules reads: "For the indication of the name (unitary, binary, or ternary) of a group to be accurate and complete, and in order that the date

may be readily verified, it is necessary to cite the author who first published the name in question." This is plain speaking and common sense. A taxonomic name is a label, no more, no less. If this were not so, names untrue to the characters or to the history of the group naturally ought to be changed. There would be no end to such changes, of course, because every age understands characters and histories in a different light. It is patent, moreover, that the Rules wish to have this label complete, that is, filled with the data making it possible to ascertain without doubt and delay its author and origin. Synonymies were in use long before Linnaeus, and even the oldest among them are careful to state the authorities of the names, this statement being an essential requirement in any citation. Nor is this all: it is only by reference to citations and authorships that priority can be determined.

The same weakness reappears in the statement just quoted from "Art. 30 a" which is manifest in its opening declaration. This weakness consists in the neglect of what the existing Rules say, and in the failure to indicate *how* the proposed reform is to work. Taking "Art. 30 a" at its word, I might not write down on paper such citations as: *Manihot gracilis* Pohl var. *genuina* Muell.-Arg. in DC. Prodr. **15**(2): 1065. 1866; or: *Mallotus oreophilus* α *ochraceo-albidus* Muell.-Arg. in op. cit., 964; but the fact that I could not legitimately write these data would certainly not free me from the duty of knowing precisely where and by whom these trinomials have been published. In cases involving doubt or possible controversy should I write such copy as this: "*Manihot gracilis* Pohl var. .....—I am forbidden by Art. 30 a (now happily in vigor) to use the original trinomial *genuina* of ..... (authorship cannot be given). I propose, consequently, in obedience to said Article a new variety *gracilis*. If somebody is to cite this variety, let him understand that Art. 30 a forbids him to reveal that I am the author of this name, and that the page and work in which I write this cannot be referred to"? Or shall I write this: "*Manihot Toledii* var. *Toledii* ..... If the reader wishes to know whether I am right in spelling *Toledii* instead of *Toledi*, will he please look ..... (authority and citation not to be given under Art. 30 a)"?

What do the proponents and authors of "Art. 30 a" mean when they speak of "*nomenclatural purposes*"? What does it mean that "*A subspecific group has no authority and no citation*"? How is an author to avoid "*authority and citation*" when he uses a taxonomic name, since such a name has definitely been published somewhere by somebody? Even tolerably precise and sound generalities are void of sense when the means are not given to work them against concrete cases; how are we, then, to use vague and unsound generalities?

(3) ". . . *For nomenclatural purposes this epithet . . . can not be transferred, except as the species to which it is subordinate may be transferred. . . .*"

A statement similar to the one quoted is contained in the current Art. 18, this Article being a peculiar compromise between different concepts of type. Article 18 reads: "A nomenclatural type is that constituent element of a group to which the name of the group is permanently attached, whether as an accepted name or as a synonym." It is true that Art. 18 declares that the nomenclatural type of a species is a specimen, description, or figure, but it is none the less true that Art. 18 hardly knows its mind. Witness the *Note* which is an integral part of this Article and says: "The nomenclatural type is not necessarily the most typical or representative element of a group; it is merely that element with which the name of the group is permanently associated." If, as Art. 18 declares, a specimen is indeed the nomenclatural type of a species, the *Note* in question is straight nonsense. A specimen *certainly* is the "most typical or representative element" of a species which is known from a single collection. To make the point clear: how can *Rose 18658* fail to be the "most typical or representative element" of *Trichocereus peruvianus*, when *T. peruvianus* solely rests upon *Rose 18658?* As a matter of fact, Art. 18 refers in its *Note* to a nomenclatural type which is certainly not a specimen, thus belying its own definition. This Art. 18 does because it tries to effect an unsuitable compromise between different concepts of type, confusing as one, (a) a type-circumscription; (b) a type-specimen; (c) a biological type. The *Note* in Art. 18 states in reality that the type subdivision (type-trinomial or type-binomial, type-genus or type-family) is not necessarily the most typical or representative element of the group (species, genus, family, or order) in the biological sense. It is merely that element to which the name is permanently attached. To exemplify: *Planta una* var. *typica* is not necessarily the most typical or representative element of the biological complex understood as *P. una*. It is merely the trinomial that cannot be transferred out of *P. una*. Clearly, specimens have nothing to do with this, nor have descriptions and illustrations.

Although illuminating and interesting, the history of Art. 18 cannot now be told because it is not germane to the subject immediately at hand. Suffice it to say that this Article appeases, without effectively compromising, two historic concepts of type, the American revolving around *type-specimens*, and the classic European centering around *type-names*. Readers who may be inclined to doubt the existence of these concepts are referred to a good authority, Greenman (Bull. Torrey Club **67**: 372. 1940), who is qualified to speak by his mature experience with both European and American botanical thought and usage.

Article 18, indirectly and imperfectly, it is true, but none the less effectively takes care of the dictum of "Art. 30 a" when it states that the nomenclatural type and the group for which it stands are "permanently attached." Obviously, the attachment being permanent, the nomenclatural type (for

instance, *Planta una* var. *typica*) and the group for which it stands (*P. una*) cannot be transferred apart, but must be moved together. Article 18, as a matter of the record, goes so far as to specify that the permanency of the attachment endures even if the nomenclatural type and its group are synonyms of other names; which is redundant, as it may not occur to anybody having any smattering of nomenclature to put *P. una* in synonymy and to treat *P. una* var. *typica* as valid or legitimate. It is patent that "Art. 30 a" is not needed, but a redefinition of Art. 18 is much to be desired, purging this Article of the contradictions which make of it a water-logged wreck rather than a trim vessel.

(4) "*Each subspecific group which includes the type of the next higher subspecific group but which excludes the type of the species shall be designated by the valid subspecific epithet of the next higher group.*"

This declaration has moved me to appreciate at long last the wisdom of the saying that the Rules should be let alone to prove themselves for a thousand years. Several months of meditation have not cleared in my understanding the purposes of "Art. 30 a" in respect to the statement just quoted. I am dubious as to my interpretation of it, and only time, long time, will tell whether I have succeeded in piercing the veil of Isis and really approached the sanctum. Naturally, I offer my interpretation of this part of "Art. 30 a" for what it is worth, and shall willingly stand corrected if I have failed to clutch its vitals.

If I read this prose aright, I understand that *Planta quaevis* subsp. *una*, which is not the type-subspecies of the binomial, this being *P. quaevis* subsp. *quaevis* (or *typica*, *genuina*, or the like), can have as its typic variety only *P. quaevis* var. *una*. In other words: the principle would seem to be reaffirmed here that *P. quaevis* shall have as its typic trinomials only subsp. *quaevis*, var. *quaevis*, and forma *quaevis*, whereas *P. quaevis* subsp. *una* shall be followed by such typic trinomials as var. *una* and forma *una*.

If this is the case, "Art. 30 a" displays praiseworthy consistency, its standards in this particular respect being higher than those of Art. 18, which roundly contradicts itself. However, the very same objection rises here that I have invoked before, namely, every trinomial which fails to comply with "Art. 30 a" is made illegitimate. The point does not need to be elucidated and discussed once again. I will emphasize the fact, however, that it is not easy to handle chains of trinomials, and that to make this handling twice as difficult by enforcing unnecessary shibboleths is hardly an evidence of wisdom. The principle that best serves here is, on the contrary, that arbitrary shackles must not be provided to hamper individual freedom in cases that are in themselves hard to manage. Let things stand as they are, so long as it is not absolutely necessary to modify them. Houses of cards are not made steadier by tinkering around the corners in order to have all edges running

true to perpendicular. Such houses look better in theory when they are straightened up, but in practice they fall to the ground. Anybody who handles as his daily fare the trinomials of Briquet, Hackel, Ascherson & Graebner, Mueller Argoviensis, and such past masters in the use of halftones will not feel kindly disposed toward hands that reach out to make the game harder than it is. To abstain from reforms which are both unnecessary and unwanted is the earmark of a philosopher.

It seems hardly necessary to discuss the "Argument" that bolsters "Art. 30 a." Only two statements in it may be paid cursory attention for the sake of a well rounded analysis. Quoth the "Argument" this much: ". . . *Proposal II does away with the use of such terms as* typica, originalis, *and the like, all of which have occasionally been misinterpreted as indicating the phylogenetic type of the species. . . . Since subspecific groups are not included in the Index Kewensis, this proposal simplifies nomenclatural investigations in taxonomic work and, since authorities are not cited, it obviates cumbersome double citations for many subspecific groups.*"

The fact that *typicus, genuinus* and the like have been occasionally misinterpreted as indicating the phylogenetic type of species, or other things, does not prove that these epithets should be blotted out, granted that it were possible to do so, which it is not. It merely means that those who abuse these trinomials and misunderstand them should be properly instructed by competent teachers, and forever furnished Articles and Recommendation that are well conceived and thoughtfully worded. The fact that a knife cuts one's finger when mishandled does not constitute a valid reason why a turkey should be torn to pieces by hand instead of being neatly carved with good steel. Since the Index Kewensis does not list subspecific epithets, and trinomials are as a rule much harder to trace back than binomials, nothing should be done in principle to disturb them without absolute necessity. The hope that nomenclatural investigations can be simplified by withholding the citations of authorities is most peculiar, for it is only by citing these authorities fully and correctly that nomenclatural investigations can be made simpler. It might facilitate my own task not to cite authorities, but this certainly will make harder the task of my neighbor. Nor is this all: if my neighbor decides to ease his own work by following my lead, it is I who stand at the receiving end. Bibliographical work is as much of a burden to a taxonomist as answering night calls is to a physician, yet each profession must be taken at its face value, putting up with its emoluments and liabilities.

In conclusion: it is certain that "Art. 30 a" is shot through by fallacies so glaring that it should be promptly withdrawn from circulation, its substance being such that it cannot be improved by hopeful manipulations. This "Article" violates in a precise and direct manner Art. 2, Art. 4, Art. 15, and Art. 46 of the Rules now in vigor, a circumstance that its authors ap-

pear to have overlooked altogether; it advances a new theory of citation which is of impossible application; it lays hands upon an Article (Art. 30) which, as will be seen, is not at all concerned with the reforms intended; it wanders aimlessly to introduce a change in the Rules which can easily be effected by a slight addition to Art. 55, which soon will be apparent; to achieve a single worth-while purpose, providing for the difficulties arising when *typicus, genuinus,* and the like are transferred, it merely repeats a dictum which is already poorly stated in Art. 18. In brief, if the simile may be forgiven, this "Article" wrecks a house in order to dig out a penny from under a table. That this "Article" is withdrawn without causing further doubts and confusion is a legitimate hope, this hope also justifying the passing in silence of all other proposals that go with "Art. 30 a," and are not better grounded than it.

The proposal of Bolle that affects the typic trinomial, although based on a misapprehension, cannot be said to be objectionable in its essence. Bolle points out in substance that when *Acomastylis elata* var. *typica* is transferred to *A. Peckii,* the resulting new combination must be *A. Peckii* var. *typica.* This combination, Bolle further points out, is erroneous because the typic variety of *A. elata* is not the typic variety of *A. Peckii.* Moved by this knowledge, Bolle asks that a Recommendation, *not an Article,* be written into the Rules to discourage the use of *typicus, genuinus,* and the like, urging on the contrary that the specific epithet be repeated. Accordingly, if *A. elata* var. *elata* is to go under *A. Peckii* a new combination results, *A. Peckii* var. *elata,* which is satisfactory.

The misapprehension in Bolle's thought arises from the fact that a Recommendation is neither retroactive nor mandatory. Accordingly, Bolle's proposed Recommendation is powerless to eliminate the inconveniences arising from the transfer of *typicus* and its equivalents, *genuinus, verus,* and the like. This Recommendation is a broken reed, and falls short of what Bolle hopes to secure from it. To elucidate the point at issue, let us suppose that a taxonomist is faced in 1952 by the problem of transferring *Manihot gracilis* var. *genuina* Muell.-Arg. (1866) to *M. tenuifolia.* This taxonomist cannot reject the variety, for it is legitimate and must, somehow, transfer it in a manner other than by moving *genuina* under *M. tenuifolia.* If Bolle had his wish come true, this taxonomist turning to the Rules to learn how to act would find therein a Recommendation urging that after 1950, let us say, no variety *genuina* should be published. Naturally, this much would not help the inquiring taxonomist in the slightest, for his interest would be to learn how to act at the moment, transferring a trinomial *genuina* legitimately published in 1866.

It is patent, consequently, that neither by forbidding the use of *typicus, genuinus,* and the like *in an Article* nor by discouraging it *in a Recommen-*

dation can the problem be solved which disturbs the authors of "Art. 30 a" and the sponsors of Bolle's "Recommendation." The solution, obviously, must be sought elsewhere. To find this solution is most easy. There is an Article in the Rules now in vigor which orders that in transferring a subdivision of a species to another species the earlier legitimate epithet must be maintained. *This is the Article*[1] *to be modified because it is the one immediately concerned with the matter.*

Article 55 reads: "When a variety or other subdivison of a species is transferred, without change of rank, to another genus or species (or placed under another generic or specific name for the same genus or species) the original subdivisional epithet must be retained or (if it has not been retained) must be re-established, unless one of the following obstacles exists: (1) that the resulting ternary combination has been previously and validly published for a subdivision based on a different type, even if that subdivision is of a different rank; (2) that there is an earlier validly published subdivisional epithet available." Shorn of technical trappings, this text means that the original specific epithet must be shifted without being changed, unless the shift creates a later homonym or a synonym. Naturally, this text orders that the trinomial *typicus,* too, be transferred, for it speaks of *all* subdivisions, without making exception for *typicus* and its kindred.

To remedy this situation, therefore, a clause must be added to Art. 55 which exempts the trinomial *typicus, genuinus,* and the like from transfers, and asks that the first meaningful epithet of higher rank be moved instead. This can be done by the following addition to Article 55: ". . . (3) that a trinomial epithet *typicus, genuinus, verus, veridicus,* or the like (cf. Rec. xviii and Rec. xxxv) is to be transferred. In this case the epithet of the name next above in rank other than *typicus, genuinus,* etc., shall be transferred . . . Examples: . . . *Acomastylis elata* var. *typica* when transferred to *A. Peckii* becomes *A. Peckii* var. *elata* not *A. Peckii* var. *typica.*—*Planta quaevis* var. *typica* f. *genuina* put under *Arbor qualis* becomes *A. qualis* var. *quaevis* f. *quaevis.*—*Frutex unicus* subsp. *quilibet* var. *originarius* moved to *Caulis magnus* is turned into *C. magnus* subsp. *quilibet* var. *quilibet.*"

This solution is liable to modifications and changes as a matter of course, if concrete evidence shows that it must be altered in detail or enlarged to take care of special cases. To discuss in full is bound to be constructive, and I shall welcome the opportunity to be shown where and how I might have

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[1] Article 55 will have to be modified at any event, for it fails to foresee the difficulties which arise when the trinomial *typicus, genuinus,* and the like are transferred in obedience to its present dicta. However, the proper place to deal with anything pertaining to types is in Section 2 of the Rules, which deals with "The type method." I refrain from discussing this Section in full here, because such a discussion would not be wholly germane to the subject under present consideration.

erred in drawing it up in its present form. It is conceivable that some reader knows of examples that have escaped my notice and bear directly upon the text here outlined. However, it may be stated that this solution, regardless of details, is simple and forcible for two reasons: (1) It directly acts upon the Article involved and does not ramble so as to lay hands upon Articles that are unrelated with the subject; (2) It takes due account of the fact that *A. elata* and *A. elata* var. *typica* are both typified by the very same specimen. Since, in the last analysis, it is this specimen which must become the type-specimen of the new variety under *A. Peckii*, it is irrelevant that the name given to this specimen is drawn from the binomial rather than from the trinomial. To elucidate: *Wallich, Sirmore & Kemaon* is the type-specimen of both *A. elata* and *A. elata* var. *typica*, while *Peck in herb. Banks.* is the type-specimen of *A. Peckii*. When *A. elata* is brought as a variety under *A. Peckii*, the new combination expressed on the basis of the specimens can be stated as follows: *Peck in herb. Banks.* has for its variety *Wallich, Sirmore & Kemaon*. It stands to reason that since the latter specimen typifies both *A. elata* and *A. elata* var. *typica*, we may use *elata* rather than *typica* as a matter of free choice, without doing violence to the inherent truth of the transfer. Naturally, the new combination *A. Peckii* var. *elata* is satisfactory. The fact that the authors of "Art. 30 a" and Bolle failed to discover this egg of Columbus seems to be due to lack of familiarity with the Rules, and with a less than perfect understanding of the nature of the trinomial *typicus*.

It is probable that some taxonomists will choose to believe that a modification of Art. 55 requires a change also in Art. 58, which—in their understanding—is supposed to order that an older valid name is transferred when the rank is changed. These taxonomists take it for granted, for instance, that when *Planta una* var. *laeta* becomes a species, the new name must be *P. laeta* comb. nov. If this interpretation be true, Art. 58 should be modified together with Art. 55 to provide for the special case involved by the transfer of *typicus* and its equivalents. It is my definite understanding that Art. 58 does not require a modification to take care of *typicus* and like epithets. However, a not irrelevant segment of botanical opinion implicitly holds to the opposite view. Naturally, I am bound to state my reasons in order that those who believe I am in error may expose the fallacies of which I am guilty, if possible, showing how Art. 58 must be modified in regard to the typic trinomial.

In the Code of Paris of 1867, Art. 58 stated: "Lorsqu' une tribu devient famille, qu'un sousgenre ou une section devient genre, qu'une subdivision d'espèce devient espèce, ou que des changements ont lieu dans le sens inverse, les noms anciens des groupes subsistent, pourvu qu'il n'en résulte pas deux genres du même nom dans le règne végétal, deux subdivisions de genre ou deux espèces du même nom dans le même genre, ou deux subdivisions du

même nom dans la même espèce." (When a tribe becomes a family, a subgenus or a section becomes a genus, a subdivision of a species becomes a species or the reverse of these changes take place, the old names are maintained so long as the result of this maintenance does not call for a later homonym of generic, specific or subspecific rank.) This text is definite to the effect that, for instance, *Magnolia virginiana* var. *foetida* L. (1753) must become *M. foetida* (L.) Sarg. (1889) as a species, the older epithet (*foetida*) persisting in the new combination. In his "Commentaires," Alphonse De Candolle, the author of this Article, states as a matter of fact (Lois Nom. Bot. 61. 1867): "Les dispositions de ces articles (*57, 58*) paraîtront nouvelles à plusieurs botanistes, du moins en ce qui concerne les modifications d'espèce. Elles sont cependant utiles pour empêcher la multiplication des noms et aider la mémoire en cas de mutation de place ou de rang. Plusieurs auteurs exacts les observent depuis longtemps." (The rulings in these Articles (*57 and 58*) will strike some botanists as novel, at least so far as they concern the remodeling of species. These rulings will serve, however, as checks upon the needless publication of new names and will provide useful reminders when names change their position and rank. These rulings are already being followed by several critical botanists.)

No one would think of using today the Paris Code of 1867 for the simple reason that, despite its fundamental nature and its inherent perfection, in it weaknesses and blemishes were revealed. For instance: Art. 56 of this Code has been dropped. It stated: "Lorsqu'on divise une espèce en deux ou plusieurs espèces, si l'une des formes a été plus anciennement distinguée, le nom lui est conservé." (When a species is remodeled into two, the binomial is maintained for that part which has [trinomially] been designated first.) This dictum was hardly sound, for it could lead to the acceptance of the first published trinomial as typic of the binomial; accordingly, Boissier's *Euphorbia Nagleri* β *baliensis* would have been typified by the trinomial *baliensis* against Boissier's own intentions in designating this variety with the letter β instead of α, the latter being accepted according to good usage as the connotation of the typic variety. Clearly, the type-variety of *E. Nagleri* is an as yet unpublished trinomial *typicus* or *Nagleri,* based upon *Nagler in herb. Berol.,* not upon *Zollinger 2975,* which is the type-specimen of β *baliensis.*

Article 58 of the Paris Code has been maintained under the same number in the International Rules of Amsterdam (1935). In the English text, this Article reads: "When a tribe becomes a family, when a subgenus or section becomes a genus, when a subdivision of a species becomes a species, or when the reverse of these changes take place, and in general when a group changes its rank, the earliest legitimate name or epithet given to the group in its new

rank is valid, unless that name or the resulting association or combination is a later homonym (see Art. 60, 61)."

This Article has been proposed for modifications and it is notoriously ambiguous. Its ambiguity, however, is not of the fundamental nature which taints Art. 18, but is due to careless editing, a blemish apparent at several points in the Rules. This Article clearly consists of two parts, namely: (1) "When a tribe becomes a family, when a subgenus or section becomes a genus, when a subdivision of a species becomes a species, or when the reverse of these changes take place, and in general when a group changes its rank, the earliest legitimate name or epithet given to the group in its new rank is valid, . . . Examples: The section *Campanopsis* R. Br. (*Prodr. Fl. Nov. Holl.* 561: 1810) of the genus *Campanula* was first raised to generic rank by Schrader, and as a genus must be called *Wahlenbergia* Schrad. (*Cat. Hort. Goett.:* 1814), not *Campanopsis* (R. Br.) O. Kuntze (Rev. Gen. II, 378: 1891).—The var. *foetida* L. (*Sp. Pl.* ed. 1. 536: 1753) of *Magnolia virginiana*, when raised to specific rank, must be called *Magnolia grandiflora* L. (*Syst. Nat.* ed. 10, 1082: 1759), not *Magnolia foetida* (L.) Sarg. (in *Gard. and For.* II, 615: 1889)—*Lythrum intermedium* Ledeb. (*Ind. Hort. Dorp.:* 1822), when treated as a variety of *Lythrum Salicaria* L., must be called *L. Salicaria* var. *glabrum* Ledeb. (*Fl. Ross.* II, 127: 1844), not *L. Salicaria* var. *intermedium* (Ledeb.) Koehne (in Engl. *Bot. Jahrb.* I, 327: 1881). In all these cases the name or epithet given to the group in its original rank is replaced by the first legitimate name or epithet given to it in its new rank."

There is not the slightest possibility of reading this text and its examples to mean that the epithet or name given to a group in a rank must be maintained in another rank. *Campanopsis, foetida, intermedium* are the *oldest names* given to a certain entity, yet these names fall against *Wahlenbergia, grandiflora* and *glabrum* which are *later names* given to the very same entity in a different rank, genus instead of section, species instead of variety, variety instead of species. Article 58 of the current Rules, consequently, unequivocally contradicts Art. 58 of the Paris Code of 1867; one says white, the other black.

Article 58 of the current Rules, however, continues after the text just quoted as follows, (2) ". . . , unless that name or the resulting association or combination is a later homonym (see Art. 60, 61)." This ending is absolutely meaningless in view of the text that precedes it. The text that precedes it—as it has been seen—flatly rules out new combinations effected to retain the older names. Why, then, anything at all should be said here about new combinations being possible later homonyms? It is understood that if *Wahlenbergia, Magnolia grandiflora,* and *Lythrum Salicaria* var. *glabrum* are later homonyms they must go, for this happens to every name in taxonomy which is a later homonym, inside and outside the purview of Art. 58.

As I have said, this meaningless and confusing addition to Art. 58 is the result of careless editing. While the *substance* of Art. 58 of the Paris Code, 1867, has been radically altered in the new Art. 58, the one saying black where the other said white, the new Art. 58 has been worded in a *form* that befits,—to a very small extent, it is true,—the old Article of the same number. Careless editing of the kind, leading to endless misinterpretations and futile arguments, is in evidence here and there in the Rules and should be corrected. What Art. 58 of the current Rules *actually* states is very plain, for the meaning of this Article is to be read in five lines of its text and in all its examples, the whole ringing as clear and as true as a bell. The obnoxious and misleading rump of this Article is one printed line that hangs in the air. *This line must go,* the sooner the better. Naturally, I do not believe that the modification I propose to introduce in Art. 55 has anything to do with Art. 58, for the two Articles are not at all germane. One (Art. 55) regulates transfers involving the *same rank* (subspecies to subspecies, variety to variety, form to form and the like); the other (Art. 58) concerns transfers effected in a *different rank* (section to genus, species to variety, variety to species), which is a very different matter. To overstress a line of print which hangs from the window sill of Art. 58 without rhyme or reason, this in order to have two basically sound Articles become confused in their purposes and ultimate concepts, is not commendable. A correction, not an "interpretation" is here in order.

It is not clear why the reformers of the trinomial *typicus* tilt with Art. 30, and attempt to plaster it with their manifestoes when this Article has basically nothing to do with *typicus*. It is peculiar, none the less, that this same Article should be widely misunderstood in other directions.

Article 30 reads as follows: "Two subdivisions of the same species, even if they are of different rank, cannot bear the same subdivisional epithet, unless they are based on the same type. If the earlier subdivisional name (ternary combination) was validly published, the later one is illegitimate and must be rejected." Some authors believe that this Article establishes the principle that all trinomials have the same rank, that is, for purposes of priority a subspecies is tantamount to a variety or a form, building on this belief strange constructions of their own making. Other authors, like the sponsors of "Art. 30 a" see in this text obscure meanings that involve the typic trinomial.

The truth is plainly otherwise and to prove it is easy indeed. Let us suppose that *Planta una* has a subspecies *rubra* (1900), and that *Arbor quaevis* has a variety *rubra* (1930), too. Let us next suppose that the var. *rubra* of *A. quaevis* is transferred under *P. una*. Effected in the usual manner this transfer gives: *Planta una* subsp. *rubra* var. *rubra*. This, Art. 30 states, can-

not be done. The reason is simple: anyone who reads this citation understands automatically that the variety is typic of the subspecies because both the subspecies and the variety have the same epithet, *rubra*. This would certainly not be true if subsp. *rubra*, for instance, were a hairy plant and var. *rubra* a glabrous one, the type-specimens of the two being different. To prevent such a confusion from arising, Art. 30 wisely arranges that var. *rubra*, which is later in point of publication, must lose its name when transferred under *P. una* and become, for instance, var. *nigra*, for the citation then reads: *P. una* subsp. *rubra* var. *nigra*, which lends itself to no ambiguity. Naturally, if subsp. *rubra* had been published later than var. *rubra*, it should be the subspecies rather than the variety to change its name. Lastly, Art. 30 allows for the case in which var. *rubra* happens to be the type-subdivision of subsp. *rubra*, making it possible to retain both without alteration.

This interpretation of Art. 30 might be challenged as overdrawn on the strength of one of the examples introduced under the Article which reads: "The following is incorrect: ***Erysimum hieraciifolium*** subsp. *strictum* var. *longisiliquum* and ***E. hieraciifolium*** subsp. *pannonicum* var. *longisiliquum*—a form of nomenclature which allows two varieties bearing the same name in the same species," nothing being stated about the transfers which I have chosen to illustrate my interpretation of the Article. This challenge deserves an answer, for it is based on the appearance of fact and works to the point.

Clearly, there should be no reason to forbid the use of var. *longisiliquum* under different subspecies of the same binomial unless for the purpose of avoiding a possible confusion between the two homonymous trinomials in question. Aside from thoughtlessness in reading the citations, which is not a matter for the Rules to take under consideration unless in the very broadest sense, such a confusion might arise in two manners: (1) By the use of an abbreviated citation such as is authorized by Art. 28. This use need not be indulged in, for Art. 28 merely states: "It is permissible to reduce more complicated names to ternary combinations. Examples— . . . *Saxifraga Aïzoon* subforma *surculosa* Engl. et Irmsch. is permissible for *Saxifraga Aïzoon* var. *typica* subvar. *brevifolia* forma *multicaulis* subforma *surculosa* Engl. et Irmsch." Naturally, no critical taxonomist will take advantage of a concession made in the Rules if this leads to ambiguity, because ambiguity is forbidden (see Art. 4); (2) By a transfer of trinomials from one species to another. Here the danger of confusion is definite, for the older epithet is transferred in principle (Art. 55) if the rank remains the same. If Art. 30 were not in the Rules, Art. 55 ought to contain its basic provisions, nevertheless. Naturally, to illustrate Art. 30 I have deliberately chosen an example that illustrates *the necessity* of this Article rather than one which shows only *its desirability*. This, I believe, is consistent with general criteria of sound

interpretation. It is obvious that Art. 30 was written by a competent student of nomenclature basically to take care of a special case. So special is this case, as a matter of fact, that Art. 30 is usually not understood, this serving as a curious illustration of the danger of feeding the best of fare to guests accustomed to coarse stew. Article 30, naturally, has nothing to do with the generalities underlying the typic trinomial and even less can it be construed to mean that all trinomials have the same rank. It will be seen that Art. 55 (1), too, vetoes the transfer of a trinomial, *regardless of its rank*, if this trinomial should prove to be a homonym. It is unfortunate that Art. 55 (1) is improperly worded, in failing to specify that it refers to trinomials *under the same species*. This, however, is rectified by the general principle contained in Art. 30.

THE ARNOLD ARBORETUM, HARVARD UNIVERSITY
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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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(exclusive of fungi)
(See also under General Botany: **Dodd & Gershoy**)

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